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IDENTIFICATION DES FACTEURS DE STRESS IMPLIQUÉS DANS LE DÉCLIN ET LA MORTALITÉ DE L'ÉRABLE À SUCRE APRÈS COUPE DE JARDINAGE

-

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HENRIK HARTMANN

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AVANT-PROPOS

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RÉSUMÉ

Le modèle conceptuel de déclin des arbres de Manion (1991) stipule que des stress dits prédisposants, d'impact modéré et agissant à long terme (ex. pollution atmosphérique), diminuent la vigueur des arbres et les rendent plus vulnérables à des stress subséquents. Ces arbres ainsi affaiblis seraient par la suite davantage affectés par des stress incitants, ces derniers ayant un impact plus prononcé et soudain (ex. défoliations d'insectes). Ceux-ci les entraîneraient alors dans une spirale de déclin vers la mort. La progression dans ce processus de déclin pouvant elle-même être accélérée par des facteurs contribuants tels les pathogènes fongiques.

La coupe de jardinage vise une amélioration de la qualité des peuplements par l'enlèvement progressif, sur plusieurs rotations, d'arbres de faible qualité et de faible vigueur, diminuant ainsi le taux de mortalité des peuplements résiduels. Récemment, l'observation d'un taux élevé de mortalité après coupe de jardinage dans la forêt publique québécoise a suscité inquiétudes et interrogations, nous incitant à entreprendre une étude afin d'identifier les causes potentielles et les processus précurseurs de la mortalité des arbres, afin de mieux comprendre ce phénomène.

Nous avons étudié près de 400 érables à sucre (*Acer saccharum* Marsh.) vivants et morts dans des érablières à bouleau jaune au Témiscamingue, Québec. Les peuplements sous étude avaient subi une coupe de jardinage en 1993-94 et tout en étant régulièrement soumis à des épidémies de la livrée des forêts (*Malacosoma disstria* Hubner).

Nous avons d'abord testé si le système de classification utilisé pour sélectionner les arbres pour la récolte pourrait être en cause dans les taux élevés de mortalité. Si le système en question ne permet pas de cibler adéquatement les arbres non vigoureux afin d'en prioriser la récolte, un mauvais choix d'arbres peut s'en suivre augmentant ainsi la proportion d'arbres non vigoureux dans le peuplement résiduel. Puisque de tels arbres sont plus susceptibles de mourir, le taux de mortalité augmenterait dans les peuplements résiduels. Nous avons comparé la probabilité de survie des arbres (évaluée à partir de leur croissance radiale récente), comme indicateur de leur vigueur réelle, entre les quatre classes de vigueur du système de classification. Nos résultats indiquent que ce système reflète assez bien la vigueur réelle des arbres et ne semble donc pas être la cause d'un mauvais choix d'arbres ni de la mortalité élevée observée après coupe.

Par la suite, nous avons évalué l'impact des perturbations associées à la coupe sur les arbres résiduels en assumant que ces perturbations pourraient imposer des stress hydriques aux arbres résiduels par les mécanismes suivants : (1) la machinerie cause de la compaction du sol et des dommages aux racines fines des arbres à proximité des sentiers de débardage ce qui pourrait engendrer, respectivement, une diminution de la disponibilité en eau dans le sol et une diminution de la capacité des arbres à puiser l'eau du sol; (2) l'ouverture de la canopée augmente la disponibilité de lumière pour les arbres, ceux-ci répondant avec un accroissement du taux photosynthétique et de transpiration ce qui intensifierait la demande en eau. Nous avons comparé les croissances radiales, les probabilités de survie et le ratio d'isotope stable de carbone ($^{13}C/^{12}C$) entre des arbres appartenant à quatre classes de

perturbation : (1) aucune perturbation, (2) perturbation de machinerie seulement, (3) augmentation de lumière seulement et (4) perturbation de machinerie et augmentation de lumière. Nos résultats montrent que les perturbations de la coupe n'ont pas eu d'impact négatif sur la croissance, la vigueur ou l'état hydrique des arbres résiduels. Au contraire, une augmentation de lumière engendrait une hausse de la croissance. La comparaison des croissances radiales entre une période de défoliation et la période suivant la coupe de jardinage démontrait que la croissance radiale était beaucoup plus faible lors de la défoliation que lors de la période suivant la coupe et ceci pour n'importe quelle combinaison de perturbations associées à la coupe.

Nous avons de plus utilisé les croissances radiales d'érables à sucre morts pour caractériser la dynamique de leur déclin. Ces arbres ont été prédisposés par une première défoliation qui les a rendu plus vulnérable à une deuxième défoliation. Une perte de vigueur importante lors de la deuxième défoliation a déclenché leur déclin final, celui-ci ayant été accéléré lors de la période après coupe. Le déclin des érables sous étude a perduré pour environ 30 ans et s'est déroulé selon le modèle de Manion (1991) : la première défoliation étant le stress prédisposant, la deuxième le stress incitant et les perturbations associées à la coupe agissant comme stress contribuants.

L'ensemble de nos résultats nous permet de conclure que les perturbations associées à la coupe de jardinage ne semblent pas expliquer le taux élevé de mortalité dans le contexte de notre étude. Toutefois, les conditions climatiques estivales favorables (températures douces, précipitations abondantes) qui ont prévalu dans les premières années après les coupes de jardinage de 1993-94 pourraient avoir empêché le développement d'un stress hydrique et ainsi avoir atténué l'impact sur les arbres résiduels des perturbations associées à la coupe.

Notre étude apporte des contributions importantes à notre compréhension de la mortalité chez les arbres. Ainsi, nous avons identifié la nature du stress prédisposant dans le déclin d'érables à sucre dans des peuplements jardinés, un aspect souvent négligé dans les études de la mortalité des arbres. De plus, notre étude a permis de démontrer que le rôle d'un stress ne dépend pas de la nature du vecteur (ex. pollution atmosphérique, insectes défoliateurs) mais plutôt de l'impact que ce stress exerce sur la vigueur de l'arbre. Au niveau méthodologique, notre étude a contribué à améliorer les estimations de probabilités de mortalité (chapitre 1) et à tester une méthode simple et efficiente d'estimation de conditions de croissance (disponibilité de lumière, chapitre 3) pour des études rétrospectives.

Notre étude soulève aussi certaines questions. Par exemple, on peut se demander quel serait l'impact des perturbations associées à la coupe sur les arbres résiduels sous des conditions climatiques moins favorables que celles ayant prévalu dans notre étude (ex. étés chauds et secs dans les années suivant la coupe)? Ou sur des sites ayant des sols différents? Pourquoi les défoliations de la livrée n'ont pas eu le même impact sur tous les arbres, causant seulement un déclin temporaire chez certains arbres mais un déclin sévère menant à la mort chez d'autres individus? Est-ce que les arbres survivants ont pu mieux se défendre contre ou encore éviter complètement les défoliations? Ces questions devraient faire l'objet d'études supplémentaires afin d'approfondir notre compréhension de la mortalité des arbres.

Mots-clés : *Acer saccharum* Marsh., mortalité, stress, vigueur, probabilité de survie

Except during the nine months before he draws his first breath, no man manages his affairs as well as a tree does.

George Bernard Shaw

Of all the wonders of nature, a tree in summer is perhaps the most remarkable; with the possible exception of a moose singing "Embraceable You" in spats.

Woody Allen

INTRODUCTION GÉNÉRALE

A. Préambule

Cette étude a été effectuée dans des érablières à bouleau jaune au Témiscaminguc (Québec). Ces peuplements sont soumis à des défoliations par la livrée des forêts (*Malacosoma disstria* Hubner) à des intervalles réguliers et ont, de plus, subi une coupe de jardinage en 1993/1994. Notre étude vise à mieux comprendre le phénomène de la mortalité chez les arbres par l'identification des facteurs qui sont impliqués dans le processus de la mortalité de l'érable à sucre et la caractérisation de leur mode d'action en interaction.

Comme nous le verrons dans les sections suivantes, les perturbations en forêt constituent des vecteurs de stress qui agissent sur la santé des arbres. La coupe de jardinage, un type de coupe partielle, provoque plusieurs modifications à l'environnement qui peuvent constituer des facteurs potentiels de stress pour les arbres résiduels. En premier lieu, la coupe augmente, par l'ouverture de la canopée, la disponibilité en lumière pour les arbres dégagés. Cette augmentation peut entraîner, pour certains arbres, une hausse soudaine et importante de la demande en eau dû à un accroissement marqué de la transpiration. Ceci pourrait donc perturber l'équilibre établi entre la biomasse foliaire et racinaire et engendrer un stress hydrique. De plus, l'utilisation de la machinerie forestière lors des opérations de récolte cause des perturbations du sol (ex. compaction) et des dommages aux systèmes racinaires des arbres ce qui peut réduire la disponibilité en eau dans le sol et la capacité d'absorption d'eau des arbres. Finalement, les perturbations naturelles, notamment les épisodes de défoliation par la livrée des forêts, peuvent être sources de stress importants pour les arbres en réduisant significativement et de façon récurrente leur biomasse foliaire et donc, par le fait même, leur potentiel photosynthétique, ce qui se traduit le plus souvent par une diminution notable de la croissance radiale.

Notre étude examine l'impact des perturbations soit naturelles ou humaines (par la coupe) sur la santé des arbres. En utilisant une approche rétrospective et en s'appuyant sur des données dendrochronologiques, cette étude nous a permis de caractériser la dynamique

entre ces facteurs de stress et d'obtenir un aperçu de l'effet cumulatif des divers stress sur la santé des arbres à l'étude.

Dans cette introduction nous allons revoir le concept de maladie et de déclin des arbres, ce qui sera suivi par un bref aperçu des mesures utilisées pour quantifier la vigueur des arbres. Nous allons aussi définir la problématique sous-jacente à notre étude en la plaçant dans son contexte théorique et pratique. Par la suite, les objectifs généraux et spécifiques de l'étude, sa structure et l'approche méthodologique seront présentés.

B. La maladie et le déclin des arbres

Les arbres sont des organismes exceptionnels. Ils atteignent des tailles impressionnantes, dépassant largement toute autre forme de vie, et peuvent vivre plus longtemps que tout autre type d'organisme. L'arbre vivant le plus âgé, un pin de Bristlecone (*Pinus longaeva* [D.K. Bailey]), a été daté à 4723 ans en 1957 (Schulman 1958). De plus, par le biais de la reproduction végétative, certaines espèces d'arbre peuvent éviter la mort de l'individu (défini par son assemblage génétique) apparemment indéfiniment. Par exemple, le peuplier faux-tremble (*Populus tremuloides* [Michx.]) peut former des colonies clonales (ramets) de grande superficie et de grand âge. Le ramet 'Pando' de cette espèce, situé dans l'état de l'Utah (E.-U.), compte plus de 47 000 tiges (ortets) sur plus de 77 hectares et son âge a été estimé à plus d'un million d'années (Mitton & Grant 1996).

Mais mêmes les arbres les plus longévifs ne vivent pas éternellement. Quoique le concept de sénescence ne semble pas s'appliquer à certaines espèces d'arbres comme le pin de Bristlecone (Lanner et Connor 2001) ou le *Thuja occidentalis* (L.) (Larson 2001), des évènements catastrophiques tels des feux de forêt, des épidémies d'insectes ou encore des chablis peuvent affecter de grandes étendues de forêt et causer la mortalité à grande échelle (ex. Solomon et al. 2003, Bouchard et al. 2005, Peterson & Pickett 1995). De plus, les arbres individuels peuvent être soumis à des stress externes qui détériorent leur état de santé, causent des maladies et mènent à leur mort. La maladie, au sens large, constitue une condition anormale de l'organisme qui perturbe son fonctionnement.

Quoique des pathogènes soient souvent des vecteurs de maladie, c'est une interaction de plusieurs facteurs qui mène à la maladie et à la mort d'un arbre et ces divers facteurs ne peuvent pas être facilement séparés les uns des autres (Franklin et al. 1987). Souvent la cause ultime de la mort d'un arbre, un déséquilibre entre le gain et les dépenses de produits photosynthétiques, peut être initialement déclenchée par une défoliation d'insectes (export de carbone par l'enlèvement de l'appareil photosynthétique) mais par la suite résulter d'un affaiblissement (ex. épuisement de réserves de carbone) de l'arbre à long terme (Franklin et al. 1987). Ainsi, le déclin des arbres est un processus complexe et graduel qui comprend plusieurs facteurs et vecteurs de stress (Waring 1987).

Manion (1991) a décrit le développement d'une maladie chez un arbre comme résultant d'une relation triangulaire entre l'hôte (arbre), les pathogènes et l'environnement. L'environnement et les pathogènes exercent des stress sur l'hôte, ce qui a pour conséquence de réduire sa vigueur. Une fois affaibli, l'hôte devient plus vulnérable à d'autres stress qui l'affaiblissent davantage et qui peuvent l'entraîner dans une spirale de déclin irréversible.

Le concept de vigueur est quelque peu ambigu et souvent utilisé comme synonyme au concept de vitalité (voir Dobbertin 2005). Selon Shigo (1986), la vitalité d'un arbre est son état de santé à un moment donné, découlant d'une interaction dynamique entre l'arbre et son environnement, notamment les stress, tandis que la vigueur d'un arbre est sa capacité génétique à survivre à de tels stress. Cette définition de vigueur est théorique et difficile, voire impossible à quantifier. Manion (1991) utilise le terme vigueur avec la signification de vitalité et cette utilisation du terme a été reprise par d'autres auteurs (ex. Kaufmann 1996, Pedersen 1998). Dans notre étude, nous adoptons la définition de vigueur de Manion (1991) afin de quantifier, à tout moment dans la vie d'un arbre, son état de santé comme une réponse à des stress environnementaux.

Selon le modèle conceptuel du déclin des arbres de Manion (1991), des **stress prédisposants,** ayant un impact modéré et agissant à long terme, diminuent la vigueur initiale des arbres. Par exemple, la pollution atmosphérique près de centres industriels a des effets toxiques sur les processus physiologiques végétaux et réduit le taux de croissance des arbres (Ashby & Fritts 1972, Pandey & Pandey 1994, Bressan 1998). Une réduction de croissance est généralement associée à une baisse de la mise en réserve de carbone sous

forme d'amidon. Chez les arbres, la mise en réserve d'amidon constitue une priorité d'allocation moins élevée que la croissance (Oliver & Larson 1996) et on suppose que seul le carbone non utilisé pour la croissance est disponible pour la mise en réserve (Le Roux et al. 2001). Ainsi, le déclin de la vigueur des arbres est généralement relié à un épuisement des réserves de carbone (Liu & Tyree 1997). Suite à une telle réduction des réserves de carbone, les arbres ne peuvent produire suffisamment de composés de défense contre des herbivores (Dunn et al. 1987) ou refaire le feuillage consommé par des herbivores (Renaud & Mauffette 1991).

Les arbres ainsi affaiblis sont plus vulnérables aux stress subséquents tels des épidémies d'insectes défoliateurs. Des défoliations répétées diminuent continuellement les réserves de carbone (Parker & Houston 1971, Gregory & Wargo 1986, Renaud & Mauffette 1991), permettant aux **stress contribuants**, tels les champignons, de vaincre les mécanismes de défense de l'hôte, accélérant ainsi son déclin (Wargo & Houston 1974) et l'entraînant dans une spirale vers la mort (Fig. I.1).

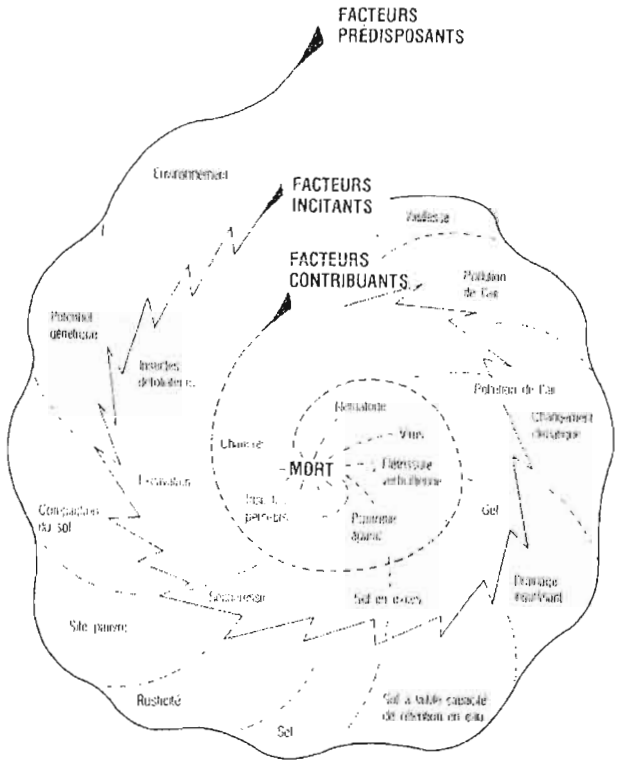

Figure I.1 La spirale de déclin des arbres de Manion (1991). Des stress prédisposants agissent à long terme sur la vigueur des arbres en les affaiblissant, les rendant ainsi plus vulnérables aux stress incitants qui, eux, sont soudains et causent une diminution abrupte de la vigueur. Des facteurs contribuants accélèrent quant à eux le déclin des arbres en perdition (Figure tirée de Innes 1994).

Ce modèle conceptuel du déclin décrit donc la mort d'un arbre comme étant le résultat d'un processus dynamique et dans lequel plusieurs facteurs jouent un rôle interactif, ce processus pouvant être de longue durée. Même avant l'apparition de symptômes visuels de déclin (ex. dépérissement de la cime), la croissance radiale peut subir des diminutions sur plusieurs années, voire même des décennies (Duchesne et al. 2003). En effet, il peut s'écouler un long moment entre le déclenchement du déclin d'un arbre par un stress incitant (ex. une sécheresse) jusqu'à ce que la mort ne survienne (Pedersen 1998).

C. Comment quantifier la vigueur des arbres ?

Il existe une panoplie de mesures pour quantifier l'état de santé d'un arbre, comme par exemple la taille des aiguilles, l'émission de luminescence ou de composés gazeux par les feuilles, ou la résistance électrique du cambium (voir Gehrig 2004). Toutefois, ces mesures sont coûteuses, difficiles à effectuer sur le terrain et ne décrivent que l'état actuel d'un arbre, ne se prêtant donc pas aux études rétrospectives.

Les cernes de croissance offrent, par contre, une source de données à résolution annuelle et peuvent donc fournir de manière retrospective des informations au sujet des conditions environnementales qui prévalaient et de l'état physiologique des arbres au moment de la formation du cerne (Saurer et al. 1997, McCarroll & Loader 2004).

La quantité de réserves de carbone contenues dans le tronc (cernes) ou les racines semble corrélée à la vigueur des arbres (Wargo 1999), mais les réserves de carbone sont difficiles à quantifier et relativement peu utilisées dans les études sur le déclin et la mortalité des arbres. Par contre, les cernes de croissance des arbres constituent une information sensible de la vigueur des arbres car la priorité d'allocation de carbone aux cernes du tronc est inférieure à la priorité d'allocation aux autres fonctions vitales telles la respiration, la croissance des racines fines, la reproduction et la croissance primaire (en élongation) (Waring 1987, Oliver & Larson 1996). Ainsi, la croissance secondaire (radiale) est habituellement l'une des premières fonctions affectées par une diminution du budget de carbone de l'arbre (Givnish 1988) et elle constitue donc un indicateur précoce d'une perte de vigueur globale de l'arbre.

Il est reconnu qu'il existe un lien entre la croissance radiale et le risque de mortalité des arbres (Wyckoff & Clark 2000). Ce lien a aussi été utilisé pour estimer des probabilités de mortalité (Monserud 1976) et a été intégré dans des modèles de simulation forestière (ex. Botkin 1993, Pacala & Hurtt 1993, Pacala et al. 1993 & 1996, Loehle & LeBlanc 1996). De plus, plusieurs études ont évalué à l'aide de cernes de croissance l'impact de stress environnementaux sur les arbres (ex. Pedersen 1998&1999, Ogle et al. 2000, Suarez et al. 2004) et l'estimation de probabilités longitudinales[1] de mortalité a été utilisée pour prédire

[1] Une étude longitudinale mesure une caractéristique chez un individu (ou un groupe d'individus) à différents moments dans le temps. Ainsi, l'étude longitudinale de séries de croissances radiales permet d'estimer des probabilités de survie à différents moments de la vie d'un arbre contrairement aux études

l'incidence de la mort des arbres (Bigler & Bugmann 2004). Dans le cadre de la présente étude, nous utilisons la croissance radiale dans le but d'estimer la probabilité longitudinale de survie des arbres afin de quantifier leur vigueur.

D. Contexte de l'étude

Cette étude vise à améliorer la compréhension du phénomène de la mortalité des arbres suite à la coupe partielle (coupe de jardinage). La coupe de jardinage, appliquée en Europe depuis plus de deux siècles (Röhrig & Gussone 1990), a été introduite graduellement au Québec au début des années 1990 (mais en 1983 dans un contexte expérimental) dans le but de pallier les effets dégradants de la coupe à diamètre limite sur la qualité et la vigueur des peuplements feuillus et mixtes (Majcen et al. 1990). Ce type de coupe, effectuée dans des peuplements de structure inéquienne, réunit les caractéristiques de plusieurs traitements sylvicoles (coupe de régénération, éclaircie, récolte) dans une seule intervention (Smith et al. 1996). La coupe de jardinage a pour objectif, en outre, l'amélioration de la qualité du peuplement résiduel en récoltant des arbres de moindre vigueur et elle vise également à diminuer les 'pertes' dues à la mortalité et donc le taux de mortalité avant la prochaine intervention.

Le rendement de la coupe de jardinage, en terme de croissance et de taux de mortalité, a été établi à partir de données récoltées dans des dispositifs de recherche gouvernementaux. Toutefois, puisque les coupes effectuées dans ces dispositifs l'ont été avec plus de soins que lors d'opérations forestières industrielles normales, une extrapolation de leurs résultats à des forêts sous aménagement industriel ne semble pas valide (Majcen 1996). Un dispositif de suivi a été installé pour vérifier le rendement réel de la coupe de jardinage dans un contexte industriel et les résultats de ce suivi ont révélé que le rendement cinq ans après la coupe (accroissement annuel périodique net) n'atteignait que 40% des prédictions basées sur les données des dispositifs expérimentaux. Ce faible accroissement serait dû à un taux de

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transversales qui sont ponctuelles et produisent des estimations seulement pour un instant donné de la vie d'un arbre.

mortalité deux fois plus élevé que dans les dispositifs de recherche (Bédard et Brassard 2002).

E. Causes potentielles des forts taux de mortatlié enregistrés

a. Mauvais choix d'arbres pour la récolte

Il a été suggéré que les normes de sélection des arbres à récolter lors de la coupe de jardinage déterminant le choix des arbres à récolter pourraient être trop vagues ou ne pas être basées sur des critères adéquats, permettant ainsi aux aménagistes de récolter des arbres vigoureux en laissant une proportion importante d'arbres non vigoureux dans les peuplements (Meunier et al. 2002). Évidemment, ces arbres résiduels peu vigoureux seraient alors plus susceptibles de mourir, ce qui pourrait expliquer le taux élevé de mortalité enregistré après jardinage. Bien que semblant intuitivement justifiée, cette explication est difficile, voire impossible à vérifier rétrospectivement et n'apporte pas d'éléments à la compréhension des mécanismes de mortalité. Toutefois, afin d'exclure le mauvais choix de tiges comme explication des forts taux de mortalité, nous allons vérifier si le système de classification des arbres actuellement en usage permet réellement de choisir des arbres à récolter selon leur vigueur.

b. Les perturbations d'arbres résiduels par la coupe partielle

La coupe partielle modifie l'environnement des arbres résiduels et ceux-ci peuvent être perturbés par ces modifications soudaines des conditions environnementales. Les modifications des conditions environnementales résultant de coupes partielles sont de plusieurs types et incluent notamment les perturbations du sol par la machinerie et l'ouverture soudaine de la voûte forestière :

- Perturbations par la machinerie forestière

La machinerie forestière exerce, selon sa masse opérationnelle, le type et les dimensions du système de traction, des pressions importantes sur le sol (Deschênes 1989) auxquelles s'ajoutent des forces de cisaillement et de vibration (Gjedtjernet 1995, Kozloswki 1999). Ces

forces causent une réduction de la porosité du sol, augmentant ainsi sa densité, détruisent la structure du sol en diminuant sa conductivité hydrique (voir revue dans Kozlowski 1999 et Lipiec & Hatano 2003) et peuvent mener à une capacité réduite de rétention d'eau dans les sols à texture fine (Souch et al. 2004). Quoique la sévérité de l'impact de ces forces varie selon les caractéristiques du sol (Assouline et al. 1997), elles réduisent généralement l'infiltration d'eau, le drainage et l'aération du sol (Taylor & Brar 1991, Herbauts et al. 1996, Starsev & McNabb 2001) et résultent, dû à une résistance à la pénétration plus élevée, en la formation de systèmes racinaires réduits et superficiels (Wronski 1984) menant à une absorption réduite d'eau au niveau de la plante (Lipiec & Hatano 2003). L'impact négatif sur le sol se produit en grande partie après un seul passage (Williamson & Neilsen 2000) et peut causer des stress hydriques et une réduction de croissance chez les arbres (Helms &Hipkin 1986, Clayton et al. 1987, Smith & Wass 1994, Tardieu 1994, Souch et al. 2004). De plus, la compaction du sol, en réduisant la capacité d'absorption de l'eau par les racines fines, réduit la capacité de transpiration des arbres (Komatsu et al. 2007) ce qui peut entraîner une diminution de la photosynthèse et éventuellement de la croissance des arbres (Law et al. 2002).

Puisque les études sur les systèmes racinaires étant fastidieuses et coûteuses, les connaissances demeurent limitées concernant les impacts directs (dommages mécaniques) de l'équipement forestier sur les racines (ex. Rönnberg 2000) ou leur impact sur la croissance globale des arbres (Waesterlund 1989, Gjedtjernet 1995), mis à part quelques évidences indirectes et anecdotiques (ex. Wronski 1984, voir aussi revue dans Trame & Harper 1997). Lagegren & Lindroth (2004) ont démontré que des arbres situés à proximité de sentiers de débardage avaient des accroissements en surface terrière moins élevés que les arbres ailleurs dans un peuplement de *Pinus sylvestris* (L.) et *Picea abies* (L.[Karst]) mais sans établir la relation entre la distance au sentier et la croissance des arbres. Ouimet et al. (2005) ont quant à eux trouvé une relation significative entre la distance des arbres par rapport à des tranchées d'excavation (pour l'enfouissement de tubulures de transport de sève d'érable) et la croissance radiale de l'érable à sucre quand cette distance était inférieure à un seuil critique (≤ 6 cm pour chaque cm de diamètre à la hauteur de poitrine, Ouimet et al. 2005).

L'impact des dommages racinaires sur la santé des arbres a été évalué surtout sur des plants d'arbres. Par exemple, Deans et al. (1990) et McKay & Milner (2000) ont démontré que des dommages racinaires causés par une manutention indélicate (ex. échappement sur le sol) de plants peut ralentir leur développement ou même entraîner leur mort (Kauppi 1984, McKay et al. 1993). En forêt, les forces mécaniques dans le sol par mouvement de masse lors d'un gel ont été tenues responsables pour des dommages et la mortalité de racines fines (Tierney et al. 2001).

Nadezhdina et al. (2006) ont démontré que le passage de la machinerie lourde à proximité des arbres diminue la conductivité hydrique et endommage le système racinaire. Quoique la régénération des racines fines soit un processus assez rapide dans des sols non perturbés (Hendrick et Pregitzer 1992), la compaction du sol par la machinerie peut nuire à cette régénération en limitant le taux de croissance racinaire (Lipiec & Hatano 2003) entraînant ainsi une contrainte persistante à l'absorption d'eau.

- Ouverture soudaine de la voûte forestière

L'éclaircie d'un peuplement forestier réduit la densité des arbres dans le but de concentrer les ressources (eau, lumière, minéraux, espace) sur un nombre réduit d'arbres résiduels (Smith et al. 1996). Bien que l'augmentation de la disponibilité en lumière puisse être bénéfique aux arbres résiduels, le fait que cette augmentation soit forte et soudaine peut perturber l'équilibre entre les racines et le feuillage (Kneeshaw et al. 2002) et avoir des effets sur l'efficacité d'utilisation de l'eau (Warren et al. 2001). Des semis sous la canopée, acclimatés à une faible luminosité, réagissent à une augmentation de la radiation avec un taux plus élevé de photosynthèse après une brève période d'inhibition (Lovelock et al. 1994, Krause et al. 2003) et une augmentation du taux photosynthétique a été également constatée pour des érables à sucre matures à proximité de trouées d'éclaircie (Jones et Thomas 2007). Toute augmentation du taux photosynthétique nécessite forcément une augmentation de la conductance stomatale afin de faciliter la diffusion de CO_2 dans les feuilles. Ceci entraîne également une augmentation de la transpiration et des besoins en eau de l'arbre (Bréda et al. 1995). Évidemment, si l'augmentation de la demande en eau est jumelée à une réduction de l'absorption d'eau, par l'intermédiaire de la compaction et/ou des dommages aux racines

fines, les arbres affectés pourraient éprouver un déséquilibre entre demande et approvisionnement en eau et subir un stress hydrique.

c. Les perturbations naturelles : défoliations par la livrée des forêts

Pour la région et l'espèce sous étude, une des perturbations naturelles importantes est due aux défoliations par la livrée des forêts. Ces épisodes de défoliation surviennent selon un cycle d'environ 9 ans et plus (MRNFPQ 2002). L'érable à sucre est l'essence-hôte préférée parmi les espèces présentes dans les peuplements sous étude (Fitzgerald 1995).

Les œufs de la livrée éclosent tôt au printemps au moment de l'ouverture des bourgeons et les larves commencent immédiatement à consommer les jeunes feuilles. Habituellement, l'impact d'une défoliation sur un arbre vigoureux est peu menaçante pour la survie de l'arbre mais des défoliations répétées sur plusieurs années peuvent réduire la croissance radiale des arbres affectés et même causer la mort de branches et de rameaux (CFS 2001). Les arbres défoliés rétablissent habituellement leurs cimes au cours de l'été mais ceci cause un épuisement des réserves de carbone (Wargo et al. 1972, Wargo 1981) ce qui entraîne des réductions de la croissance radiale (Gross 1991) et rend les arbres affectés plus vulnérables à des stress subséquents (Renaud & Mauffette 1991).

F. Les mécanismes anticipés

En résumé, les perturbations du sol par la machinerie lors des opérations de récolte sont susceptibles de causer une diminution de la disponibilité en eau dans le sol et d'engendrer une contrainte à l'absorption de l'eau par les racines. D'autre part, l'ouverture de la canopée est susceptible de causer une augmentation de la transpiration et donc un accroissement du besoin en eau des arbres. Les impacts de ces deux perturbations sont potentiellement additifs et sont susceptibles de causer des déficits hydriques chez les arbres affectés. Nous avons donc avancé l'hypothèse que ces perturbations pourraient, surtout quand elles sont jumelées, causer des stress hydriques assez sévères pour déclencher un déclin et potentiellement la mort des arbres affectés.

N'oublions pas qu'à ces perturbations s'ajoutent les impacts des défoliations de la livrée. Selon le modèle de Manion (1991), les défoliations pourraient, selon leur sévérité, agir comme facteur de stress dans le déclin des arbres. Alors, la réponse des arbres aux perturbations de la coupe devrait être plus négative s'ils ont été affectés par une défoliation peu de temps auparavant, durant ou après la coupe. Puisque les défoliations diminuent la quantité de réserves de carbone, les arbres défoliés devraient être moins en mesure de contrer les impacts des perturbations associées à la coupe, par exemple pour rétablir et/ou augmenter leur réseau de racines fines afin d'assurer un approvisionnement en eau suffisant.

G. Objectifs généraux de la thèse

Cette thèse vise deux principaux objectifs. Le premier est d'identifier les causes potentielles du taux de mortalité élevé observé dans des peuplements dominés par l'érable à sucre et suite à des coupes de jardinage. Le deuxième est de décrire les interactions entre les perturbations associées à la coupe, les perturbations naturelles et la vigueur des arbres et ce afin d'acquérir une meilleure compréhension des mécanismes et processus de la mortalité des arbres.

H. Objectifs spécifiques de la thèse

- Développer et tester la performance d'une méthode de traitement de données dendrochronologiques permettant de tenir compte de l'influence des conditions environnementales sur les estimations de la probabilité de mortalité comme mesure de vigueur.
- Vérifier la concordance entre la vigueur établie à partir d'un système de classification de la vigueur basé sur des défaults externes des arbres et la vigueur 'réelle' de l'érable à sucre établie à partir de probabilités de survie longitudinales basées sur des données dendrochronologiques.
- Évaluer et comparer l'impact des perturbations associées à la coupe de jardinage à l'impact d'épisodes de défoliation par la livrée des forêts sur la croissance radiale et

la vigueur de l'érable à sucre, et évaluer l'interaction entre ces deux sources potentielles de stress.

- Vérifier si les perturbations associées à la coupe de jardinage (perturbations du sol, augmentation de la disponibilité de lumière) causent un stress hydrique chez les arbres résiduels.

I. Approche méthodologique et structure de la thèse

La thèse comporte quatre chapitres. Afin de tenir compte des délais qui peuvent s'écouler entre l'incidence d'un stress et la réaction de l'arbre, nous avons choisi d'entreprendre l'étude dans des peuplements ayant subi une coupe de jardinage 11 ans avant l'échantillonnage, assumant que les impacts de la coupe sur l'état de santé des arbres devraient se manifester au cours de cette période.

Le **premier chapitre** est de nature méthodologique et a été élaboré afin de répondre à une lacune observée dans plusieurs études visant à estimer la probabilité de mortalité des arbres à partir de leur croissance récente. Ce premier chapitre présente et teste une méthodologie de traitement de données dendrochronologiques pour l'estimation de probabilités de mortalité par régression logistique. Cette méthodologie vise à éliminer l'impact potentiel des conditions environnementales sur les estimations de probabilité de mortalité les rendant ainsi plus robustes pour des applications générales (ex. modélisation).

Le **chapitre deux** vise à déterminer si la vigueur établie à partir de défaults externes des arbres corrrespond à la vigueur estimée à partir de données dendrochronologiques. Ainsi, ce chapitre vise à tester le système de classification des arbres utilisé pour la sélection des arbres à récolter. Ce système a été introduit par le Ministère des Ressources naturelles et de la faune du Québec (Boulet et al. 2005) et vise à estimer la vigueur et l'espérance de survie des arbres dans le but de sélectionner pour la récolte les arbres moins vigoureux et avec un plus grand risque de mortalité. Dans ce chapitre, nous testons si les classes de vigueur du système de classification reflètent la vigueur réelle des arbres telle qu'exprimée par les probabilités longitudinales de survie. Ce chapitre nous permet donc de vérifier si le système de classification pourrait permettre un mauvais choix des arbres pour la récolte.

Au **chapitre trois**, nous vérifions si certaines perturbations associées à la coupe (i.e., la circulation de la machinerie à proximité des arbres et l'augmentation forte et soudaine de la disponibilité de lumière) affectent la croissance et la vigueur des arbres. Par un design expérimental factoriel, nous évaluons séparément l'impact de l'une ou l'autre des perturbations ainsi que l'impact de la combinaison des deux perturbations sur la croissance et la vigueur des arbres. De plus, nous comparons l'impact des perturbations associées à la coupe avec l'impact des perturbations naturelles (défoliations) sur la croissance et la vigueur des arbres et nous caractérisons la dynamique temporelle des interactions entre les diverses perturbations. En utilisant à la fois les données d'arbres vivants et morts, nous serons en mesure de décrire le déroulement temporel du déclin des arbres. Ce chapitre nous permettra donc d'identifier les facteurs de stress agissant sur l'état de santé des arbres ainsi que de vérifier si le déclin des arbres se déroule selon le modèle conceptuel de Manion (1991).

Le **chapitre quatre** présente une étude dans laquelle nous avons eu recours à l'analyse d'isotopes stables de carbone dans les cernes de croissance afin de vérifier si les traitements de coupe ont causé un stress hydrique chez les arbres résiduels. En ayant recours à un design expérimental factoriel, nous testons pour la présence d'un stress hydrique pour chaque perturbation de coupe individuellement et pour la combinaison des deux perturbations.

I. IMPROVING TREE MORTALITY MODELS BY ACCOUNTING FOR ENVIRONMENTAL INFLUENCES

Henrik Hartmann, Christian Messier & Marilou Beaudet

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1.1 Abstract

Tree-ring chronologies have been widely used in studies of tree mortality where variables of recent growth act as an indicator of tree physiological vigour. Comparing recent radial growth of live and dead trees thus allows estimating probabilities of tree mortality. Sampling of mature dead trees usually provides death-year distributions that may span over years or decades. Recent growth of dead trees (prior to death) is then computed during a number of periods, whereas recent growth (prior to sampling) for live trees is computed for identical periods. Because recent growth of live and dead trees is then computed for different periods, external factors such as disturbance or climate may influence growth rates and, thus, mortality probability estimations. To counteract this problem, we propose the truncating of live-growth series to obtain similar frequency distributions of the "last year of growth" for the populations of live and dead trees.

In this paper, we use different growth scenarios from several tree species, from several geographic sources, and from trees with different growth patterns to evaluate the impact of truncating on predictor variables and their selection in logistic regression analysis. Also, we assess the ability of the resulting models to accurately predict the status of trees through internal and external validation.

Our results suggest that the truncating of live-growth series helps decrease the influence of external factors on growth comparisons. By doing so, it reinforces the growth–vigour link of the mortality model and enhances the model's accuracy as well as its general applicability. Hence, if model parameters are to be integrated in simulation models of greater geographical extent, truncating may be used to increase model robustness.

1.2 Résumé

La dendrochronologie été largement utilisée dans les études portant sur la mortalité des arbres où des variables de croissance récente sont utilisées comme indicateur de la vigueur physiologique des arbres. La comparaison de la croissance radiale récente d'arbres vivants et morts permet donc d'estimer la probabilité de mortalité des arbres. L'échantillonnage d'arbres matures morts fournit généralement la distribution des années de mortalité qui peuvent s'étendre sur plusieurs années ou décennies. La croissance récente des arbres morts (avant leur mort) est ensuite calculée pour un certain nombre de périodes alors que celle des arbres vivants (avant leur échantillonnage) est calculée pour des périodes identiques. Puisque la croissance récente des arbres vivants et morts est ensuite calculée pour des périodes différentes, des facteurs externes tels les perturbations ou le climat peuvent influencer le taux de croissance et, par conséquent, l'estimation de la probabilité de mortalité. Pour résoudre ce problème, nous proposons de tronquer les séries de croissance des arbres vivants de façon à obtenir des distributions de fréquence similaires de « la dernière année de croissance » pour les populations d'arbres vivants et morts.

Dans cette étude, nous utilisons différents scénarios de croissance à partir de plusieurs espèces d'arbre et de plusieurs origines géographiques ainsi que différents patrons de croissance pour évaluer l'impact des séries tronquées sur les variables de prédiction et sur leur sélection dans les analyses de régression logistique. De plus, nous évaluons la capacité des modèles qui en résultent à prédire avec exactitude le statut des arbres à l'aide d'une validation interne et externe.

Nos résultats indiquent que les séries de croissance tronquées des arbres vivants contribuent à diminuer l'influence des facteurs externes sur les comparaisons de croissance. De ce fait, elles renforcent le lien entre la croissance et la vigueur dans le modèle de mortalité et améliorent l'exactitude et l'applicabilité générale du modèle. Par conséquent, si les paramètres du modèle doivent être intégrés dans des modèles de simulation à plus grande portée géographique, les séries tronquées peuvent être utilisées pour augmenter la robustesse du modèle.

1.3 Introduction

Tree mortality is a critical component of forest dynamics. Since the early 1980's, there has been a marked increase of publications related to tree mortality (e.g., Waring 1987, Franklin et al. 1987). During this period some of the earlier studies focused on predicting individual tree mortality in an empirical manner using stem diameter and diameter increment as predictor variables (e.g., Monserud 1976, Buchman 1983, Buchman and Lentz 1984).

Generally, a tree dies when it cannot acquire or mobilize enough resources to repair damage, overcome stress or otherwise sustain its life (Waring 1987). There are many potential physiological causes for a tree's decline in vigor (Franklin et al. 1987). Tree vigor is a somewhat ambiguous concept aiming to describe a tree's vitality. Tree vigor can be estimated in the field with a visual assessment of the social position of trees and morphological and pathological qualities of the tree stem, crown or bark (e.g., Ouellet and Zarnovican 1988, Millers et al. 1991, OMNR 2004) but also with measures of physiological processes (e.g., photosynthesis) or vital functions such as radial growth (Gehrig 2004). Manion's (1981) described a conceptual tree decline model in which the downward spiral towards death is often triggered by some form of disturbance or by the interacting effects of environmental factors and pathogens. If the underlying physiological processes do not yield sufficient synthate to sustain all essential vital functions, tree vigor declines. Oliver and Larson (1996) provided some insight into this concept by ranking the vital functions of a tree in order of allocation priority where maintenance of live tissue, fine root production and reproduction precede height and diameter growth. Since radial growth has a low priority in carbon allocation, it is sensitive to the overall carbon balance of a tree, and is considered to be positively correlated with tree vigor (Waring and Pitman 1985, Pedersen 1998a, 1998b). Since tree vigor itself is expected to be negatively correlated with tree mortality, radial growth has been successfully used to predict mortality probabilities (e.g., Ogle et al. 2000, Bigler and Bugmann 2003, 2004a, 2004b).

Low growth rates in dying trees is therefore information that can be used for estimating mortality probabilities using measures of 'recent radial growth' of live and dead trees (Wyckoff and Clark 2000). A tree's last year of growth, or the average growth over some period prior to death, can then be used as a predictor variable in, for example, a logistic

regression model (e.g., Flewelling and Monserud 2002, van Mantgem 2003). To account for the fact that trees with slow but steady growth can survive over long periods whereas trees with initially rapid but then decreasing growth levels often die, some authors also included growth trend variables as predictors for tree mortality models (Bigler and Bugmann 2003, Bigler and Bugmann 2004a).

When using logistic models, the prediction of individual-tree mortality probabilities requires live and dead tree growth series, from which various predictor variables, such as those mentioned above, can be computed. However, since the death of individual trees is a relatively rare event in the absence of severe or large-scale disturbance, samples of dead trees usually comprise trees that have died over a more or less wide range of years. On the other hand, the last year of growth of live individuals usually corresponds to the year of sampling or, if growth has not ceased by the time of sampling, the year prior to sampling. The anchor point for predictor variable computations (death year or last year of growth) therefore varies between live and dead individuals. This means that computed growth variables for dead trees correspond to different time windows whereas growth variables of all live individual are computed for the same period. If growing conditions change through time due to the influence of external factors (e.g. disturbance, climate) the recent growth of live trees might be subjected to the influence of factors that will not necessarily have affected the growth of dead trees, prior to their death. One can therefore expect that the difference in growth (levels and/or trends) between live and dead trees might be over-or under-estimated relative to what it would have been if it had been evaluated at corresponding periods (Fig. 1.1). Therefore, under some circumstances, the resulting estimates of mortality probabilities might be inaccurate. Other researchers have addressed this issue by explicitly modelling environmental variations and intervention occurrences (i.e. inciting stresses) that are common to all trees at a particular site and then using only estimated parameters of "vigor-related" growth variations (e.g., Pedersen 1998b). However, by relying completely on model estimates this method may be prone to add further modelling uncertainty (i.e. through model assumptions and parameter estimate uncertainties) to the resulting mortality model. Truncating constitutes a more direct method and should yield growth variables that reflect more accurately the difference in vigor between live and dead individuals, rather than the difference in growing conditions between different time windows. The resulting model is therefore expected to better reflect the

biological differences occurring between live and dead trees, reducing the need for empirical calibration (Hawkes 2000).

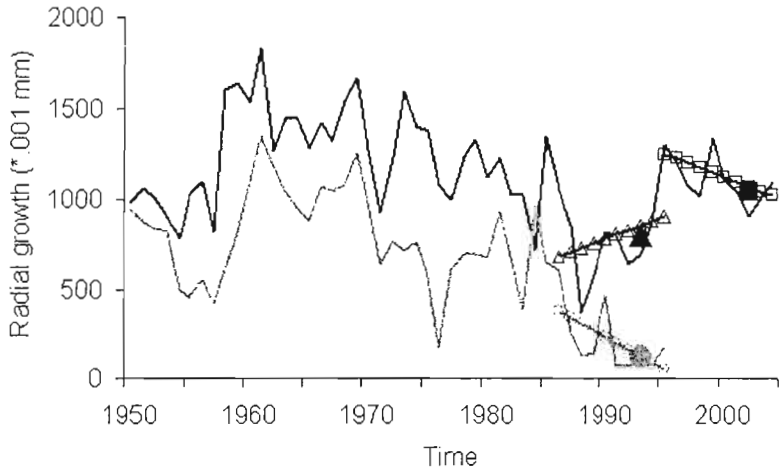

Figure 1.1 Recent radial growth series and computed growth variables for live (black line) and dead (grey line) individuals. Lines with open symbols indicate the slope of the last ten years of growth for dead (o, 1986-1995) and live (Δ, 1986-1995; □, 1995-2004) trees, solid symbols indicate the 5-yr median of 'recent growth'. Note the change in both median and slope when different time frames are used to compute the growth variables of the live tree.

In this paper, our objective was to determine if truncating (right-censoring) the growth series of each live tree to the death year of a paired dead individual would affect the discriminative ability of a logistic individual-tree mortality model. More specifically, we wanted to evaluate the magnitude, if any, of the effect that might be introduced when the proposed procedure (truncating) is not performed, and identify situations where it might be especially important to take into account. To do so, we compare models based on truncated live series with those based on untruncated data using predictor choice and validation measures as evaluation criteria.

The overall hypothesis is that the impact of truncating depends on the underlying growth dynamics of the training and validation data sets (where the training data is used to parameterize the model, while the validation data is an independent data set used to test the

model performance). Two types of validation will be performed: internal and external. Internal validation uses a resample (e.g., bootstrap sample) of the original (training) data whereas external validation is based on a completely independent data set which does not come from the same sample population (Harrell 2001). We evaluate the model on its discriminative ability, i.e. its ability to correctly predict the status (live or dead) of the trees from their growth history. We predict that, (i) an untruncated model should generally have a higher discriminative and predictive ability in internal validation if, during the years when their growth is being compared, the growth of live and dead trees shows a diverging trend over time. Here, truncating would reduce the values of growth level variables of live trees, and therefore also reduce the differential between live and growth trees. When live and dead tree growth series approach over time (merging trend), (ii) truncating should increase the internal predictive ability of the model since it causes an increase in growth level differences. Since we wish our testing to be as stringent as possible, we also use external validation. Here (iii) truncated models should have a better discriminative ability in most cases. Since truncating possibly eliminates growth variation due to data-specific external factors (e.g., disturbance, climate), it is expected to make these models more indicative of the biological processes of vigor decline preceding death which is the overall assumption of all mortality models based on radial growth.

1.4 Material & methods

DATA SOURCES

The three hypotheses were tested using five data sets corresponding to various tree species from different geographic areas: (A) White spruce (Picea glauca [Moench] Voss) from the Abitibi region in northwestern Quebec, Canada (48°30' N, 79°1' W) (Senecal et al. 2004); (B) sugar maple from the Temiscaming area (46°43' N, 79°04' W) (Hartmann, H. unpublished data); (C) balsam fir (Abies balsamifera (L.) P. Mill.), (D) black spruce (Picea mariana (P. Mill.) B.S.P.) from the lower North Shore in eastern Quebec (49°36' N, 68°39' W) (DeGrandpré, L., unpublished data); and (E) Norway spruce (Picea abies [L.] Karst.) from Pallas Yllas Tunturi in north western Finland (67°56' N, 23°44' E) (Caron, M.-N., unpublished data). These stands were of different age structures (uneven-aged, even-aged) and of different ages (approximately 70 to 150 years). The stands represented by these data sets underwent different disturbances (e.g. defoliation, drought), which produced different growth dynamics (Fig. 1.2).

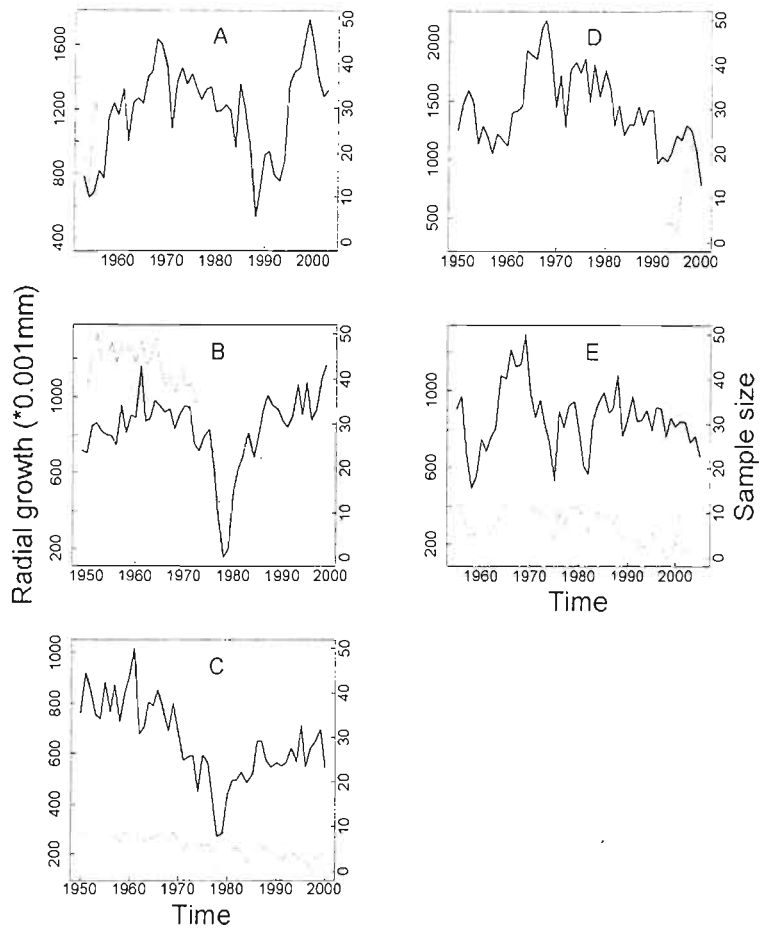

Figure 1.2 Average chronologies for live (black line) and dead (grey line) tree growth series (1950-end of series) and sample size of dead individuals (dotted line). Sample size of live trees = 30 throughout the period. Figure lettering corresponds to data set identification for the different data sets (A to E), see Table 1.1 and text for details.

In A and C the growth of live and dead trees diverges over time (at least if one considers the last 15-20 years) whereas in D and E, live and dead tree growth series show a merging or non-diverging trend. As for B, the average growth level of dead trees is lower than that of live trees before 1978 (corresponding to a spruce budworm epidemic) but shows a marked release afterwards, leading to a cross-over of live and dead tree growth series. The average number of years since death for dead trees varied from 3.9 yrs (A) to 22.9 yrs (E) (Table 1.1).

Table 1.1
Growth series identification, location, growth pattern, tree size (DBH), last entire year of growth and range of year of death of the data sets used as modelling scenarios

Data set	Location	Growth pattern ~15 - 20yrs prior	DBH range (cm)	Last entire year of growth (live trees)	Range of year of death (average time since death)
A	Temiscaming, Quebec, Canada	Diverging	19 – 42	2003	1994-2003 (3.9)
B	Lower St.-Lawrence, Quebec, Canada	Cross-over	12 – 44	1999	1974-1999 (18.3)
C	Lower St.-Lawrence, Quebec, Canada	Diverging	13 – 37	2000	1963-2000 (10.7)
D	Abitibi, Quebec, Canada	Merging	n/a	2000	1979-1999 (12.4)
E	Pallas Yllas Tunturi, Finland	Merging	n/a	2005	1938-2001 (22.9)

DATA TREATMENT

Among the sampled trees available in each data set we only used trees with diameters between 19 cm and 49 cm in DBH (diameter at breast height) as to avoid heavily suppressed (=smaller diameters) and senescent (=larger diameters) trees. Trees were selected so that the sample was evenly distributed within these diameter limits. Live trees were sampled using an increment borer at DBH whereas for dead trees, cross sections were taken at the same height. Radial increment was measured using a computer-assisted micrometer (0.001 mm precision) equipped with a microscope. Live tree growth series were used to construct a master chronology using COFECHA (Holmes 1983) and visual examination of marker years which permitted crossdating of dead individuals. Some of the growth series could not be crossdated with absolute certainty so they were excluded from our analyses. These series were mostly from heavily suppressed trees with very low growth rates and little growth variation. However, the remaining trees showed clear evidence for some kind of cyclic disturbance (i.e. spruce budworm [A, C, D] or forest tent caterpillar [B]) or very cold summer temperatures ([E]) and the associated growth declines served as reliable marker years. Based on these visual datings, COFECHA was used to detect missing or false rings which would then be identified on the cores or cross sections. After adding or removing these measurements, COFECHA was used again to verify the crossdating which usually yielded satisfactorily results.

The original data sets had varying sample sizes and, in most cases, at least two increment cores (live) or two radii on cross sections (dead) were available per tree. These tree-level

measurements were averaged to account for intra-tree variability of radial increment due to growing conditions or leaning (Kienholz 1930, Peterson and Peterson 1995). However, all the tests were run on data sets with an equal number of live and dead individuals to minimize the influence of sample size on predictive ability (Fielding and Bell 1997). To do so, we randomly selected 30 dead and 30 live individuals from each data set. As the goal of this study was not to estimate absolute mortality probabilities but rather to compare changes in discriminative ability induced by truncating within each data set, we assume that the differences in sampling strategies (e.g., coring height, use of cores vs. cross sections) do not affect the general conclusions.

Thirty live and thirty dead trees were randomly selected form each data set and paired using tree size classes as grouping factor (i.e., DBH classes: 19.1 – 29.0 cm, 29.1 – 39.0 cm and 39.1 – 49.0 cm) when information on tree size was available (sugar maple, black spruce, balsam fir). The use of these coarse classes, while controlling for diameter related growth differences, reduces the risk that live trees, after truncating and therefore reducing diameters, were paired with consistently larger dead trees. The model comparisons should still be valid even where tree size distributions could not be homogenized across live and dead trees since the same data set was used to compare the truncated with the untruncated model.

Truncating was done by snipping the growth series of a live tree to the year of death of its paired dead individual. Each of the resulting data sets contained 30 dead tree growth series and 30 live tree growth series, the latter as both truncated and untruncated series. A number of variables were computed to describe the recent growth history for each growth series: growth level variables included the medians over 3, 5, and 10 years of 'recent' growth (Med_3, Med_5, and Med_10, respectively), and growth trend variables which included the slopes calculated over 3, 5, 10, 25, and 35 years of 'recent' growth (SLP_3, SLP_5, SLP_10, SLP_25 and SLP_35, respectively). Considering that the logistic regression analyses used growth level and trend variables, we did not standardize radial growth series nor did we apply any detrending methods. Each of these data treatments would have eliminated, at least partially, the desired information.

STATISTICAL ANALYSIS

We used logistic regression to estimate mortality probabilities as a function of 'recent' radial growth variables. This method is adequate for estimating a binary dependent variable (e.g. live or dead status) from a vector of discrete or continuous variables (Hosmer and Lemeshow 2000). The logistic model is:

$$P(Y=1)=\frac{e^{\alpha G_L+\beta G_T}}{1+e^{\alpha G_L+\beta G_T}}$$

where P(Y=1) is the probability that an individual tree dies given the combination of independent variables (G_L: growth level and G_T: growth trend) and their coefficients, α and β (Hosmer and Lemeshow 2000, Quinn and Keough 2002).

Logistic regression analysis was performed in two steps for each data set. The purpose of the first step was to determine which of the many alternative univariate models, each containing one growth level variable (G_L), would provide the best fit. Parameter estimation was performed using maximum log-likelihood, and the model yielding the highest likelihood ratio was selected for further analysis. In the second step, growth trend variables (G_T) were added individually to the best univariate model, and a likelihood ratio test (LRT) was performed to determine whether the bivariate model yielded a statistically significant ($p<0.05$) improvement to the maximized likelihood over the nested univariate model (Venables and Ripley 2004). In any case, only one growth trend and one growth level variable was allowed to remain in the final model. All regression and validation analyses were performed using the statistical computing environment and language 'R' (R Development Core Team 2005).

Once a logistic model has been developed and parameters estimated using measures of 'goodness of fit' and statistical significance as decision criteria, care should be taken to further evaluate the model by assessing prediction error (Fielding and Bell 1997). Solely reporting positive and negative predictive powers of a model can yield a misleading model evaluation because such measures are sensitive to the prevalence (i.e. the relative frequency of the positive outcome) in the data as well as to the threshold used to determine the binary outcome (Manel et al. 2001). More rigorous measures such as the 'receiver operating

characteristics' (ROC) plot, developed from signal detection theory (Mason 1982), can be applied in ecological studies (Guisan and Zimmermann 2000). Hence, we used some of these measures from Harrell's (2001) contributed S-Plus libraries (`Design` and `Hmisc`) (see below) for model assessment.

When model performance is internally evaluated, i.e. using the training (parameterization) data, estimates of the model's predictive accuracy are usually optimistic (Copas 1983, Efron 1983, Van Houwelingen and Le Cessie 1990). This optimism can be accounted for using a bootstrap procedure. First, validation indices are computed on the original data set. Then, at each iteration, these indices are recomputed on the bootstrap sample. Each of the bootstrap indices minus the original indices provides an estimate of the (overfitting-induced) optimism of the original fitting process. The optimism indices are averaged over the number of iterations and subtracted from the original indices, yielding a bias-corrected estimate of the predictive accuracy. The bootstrap procedure is a very efficient means of validation since no data is withheld from the model fitting process (Steyerberg et al. 2001).

However, external validation is the most stringent means for testing the general applicability of a model to a new data set and data from a different geographic area may be used to do so (Harrell 2001). To achieve this, the models are first developed and validated with the above mentioned internal methods and the resulting best model is then 'frozen' and applied to an external data set not related to the training data.

We validated the final 'best' model internally using the bootstrap validation procedure `validate.lrm` available in the `Design` library (version 2.0-12, Harrell 2005), using Somer's D_{XY} index as criteria of model discriminative ability (Somer 1962). The latter is closely related to the area under the curve (AUC) of the ROC plot (Engelmann et al. 2003) and is, as such, independent of prevalence and classification threshold (Swets 1988). The AUC (and thus Somer's D_{XY}) is a good indicator in ecological research of responses that are naturally dichotomous, like the occurrence or non-occurrence of events such as death (Murtaugh 1996). D_{XY} values range from -1 (perfect status misclassification where the model classifies all live trees as dead and vice-versa) to 1 (perfect status classification). Values > 0.6 indicate a useful modelling application according to Manel et al. (1999). However, we added

Nagelkerke's R_N^2 as a measure of discriminative strength to have more information for model comparisons (Harrell 2001).

This internal validation was performed to obtain an unbiased (from overfitting) measure of the discriminative ability of the developed models. However, bootstrapping does not eliminate the underlying growth dynamics in each data set. Hence, external validation on an independent data set was performed to more rigorously test model discriminative abilities. Although we used data set from other tree species, the purpose was only to validate our models on other independent data sets. This external validation should be regarded only as a stringent form of model testing (Harrell 2001) and not an attempt to test whether the model is universally applicable across species. We used the `val.prob` procedure from the `Desgin` library to perform this validation. Predicted and observed probabilities were used to compute several discrimination measures (e.g., D_{XY}) where the selected model of one data set is applied with its original calibration to another.

1.5 Results

Truncating synchronizes the distribution of the last year of growth of live trees with the distribution of the year death of dead trees allowing growth comparisons of live and dead individuals to be based on variables computed over the same time period. Depending on the data set, truncating may increase (B) or decrease (E) values of the predictor variables but often no consistent pattern within a data set emerges (data not shown).

For each of the five datasets, the predictor selection of the final truncated model was different from that of the final untruncated model, but there was no obvious pattern in predictor selection (Table 1.2). There was also no clear pattern in variable selection; truncating did not yield models with either consistently longer or shorter median or trend intervals than untruncated models. In two models (C untruncated, E truncated) only the growth level variable was retained in the final model. In all other cases, the regression analyses yielded bivariate models. Similarly, parameter estimates showed no obvious pattern, truncating neither consistently increased nor decreased estimates (Table 1.2).

Internal validation also showed variable patterns in predictive (R_N^2) and discriminative (D_{XY}) ability depending on the situation. For the two data sets with diverging growth chronologies (A, C) and the data set where chronologies crossed over (B), truncating lowered R_N^2 and D_{XY} values (Table 1.2). However, for the two other data sets with merging growth trends, truncated models were of better predictive and discriminative strength (Table 1.2).

Table 1.2
Most significant variables, selected variables, and associated internal predictive and discriminative measures (R_N^2 and D_{XY}) of the 5 data sets used in the modelling procedure based on truncated and untruncated live tree growth series. Parameter estimates are given in parentheses

	Untruncated					Truncated				
Datasets	Final model			R_N^2	D_{XY}	Final model			R_N^2	D_{XY}
A	Med_10 (-0.001917)	+	Slp_25 (-0.050886)	**0.572**	**0.806**	Med_3 (-0.002641)	+	Slp_3 (-0.004504)	0.536	0.761
B	Med_3 (0.00422)	+	Slp_25 (-0.14174)	**0.645**	**0.820**	Med_5 (0.0002561)	+	Slp_35 (-0.0723448)	0.296	0.517
C	Med_3 (-0.01923)			**0.770**	**0.912**	Med_10 (-0.01596)	+	Slp_35 (0.16283)	0.740	0.883
D	Med_5 (-0.003828)	+	Slp_35 (0.028764)	0.513	0.719	Med_3 (-0.003527)	+	Slp_3 (-0.012734)	**0.648**	**0.854**
E	Med_10 (-0.08507)	+	Slp_25 (0.71304)	0.670	0.850	Med_10 (-0.08957)			**0.722**	**0.897**

Note: Bold values indicate the highest score of D_{XY} and associated R_N^2 values between the final truncated and untruncated model

External validation showed that truncating increased the predictive-discriminative strength of the models when they were applied to data sets with different growth patterns (Table 1.3). Truncated models based on A and C (both merging) performed better on D and E (both diverging) than the untruncated models. However, the cross-over growth trend from B did not yield a single good model, i.e. all models had D_{XY} values < 0.6 whether or not they were applied to similar (diverging) or dissimilar (merging) data. Untruncated models had higher discriminative ability when run on data with similar growth patterns. Good predictive-discriminative ability ($D_{XY} > 0.6$) was observed when the untruncated model from A was run on B or C or when the untruncated model of C was run on A (Table 1.3, columns 1 to 3). Also, the C model performed poorly on only B even though the higher D_{XY} and R_N^2 values of the untruncated model seems to indicate that untruncated models are more discriminative when used on data of similar growth dynamics (Table 1.3, column 3).

Table 1.3
External validation: predictive and discriminative measures (R_V^2 and D_{XY}) of untruncated (UT) and truncated (T) models developed on different training data sets when applied to the various test data sets

		Training data set									
		1		2		3		4		5	
		A (merging)		B (cross-over)		C (merging)		D (diverging)		E (diverging)	
Test data set		UT	T	UT	T	UT	T	UT	T	UT	T
A	D_{XY}	-	-	0.376	0.457	**0.731**	0.334	0.540	**0.708**	0.433	**0.631**
(merging)	R_V^2	-	-	0.144	0.166	**0.372**	0.179	0.274	**0.518**	0.203	**0.311**
B	D_{XY}	**0.706**	0.260	-	-	0.406	0.099	0.158	0.271	0.163	0.209
(cross-over)	R_V^2	**0.430**	0.105	-	-	0.178	0.001	0.039	0.097	0.019	0.069
C	D_{XY}	**0.880**	0.830	0.184	0.163	-	-	**0.900**	0.553	0.729	**0.862**
(merging)	R_V^2	**0.709**	0.651	0.028	0.002	-	-	**0.754**	0.320	0.493	**0.695**
D	D_{XY}	0.162	**0.821**	0.383	0.380	0.252	0.471	-	-	0.603	**0.683**
(diverging)	R_V^2	0.039	**0.642**	0.177	0.144	0.091	0.202	-	-	0.294	**0.452**
E	D_{XY}	0.568	**0.823**	0.559	0.116	0.741	**0.891**	**0.813**	0.691	-	-
(diverging)	R_V^2	0.294	**0.526**	0.330	0.025	0.419	**0.739**	**0.582**	0.393	-	-

Note: Bold values indicate the best (truncated vs. untruncated) model's discriminative ability (D_{XY}) with associated predictive power (R_V^2) when D_{XY} >0.6.

External validation of models based on the diverging growth chronologies (D and E) showed somewhat less obvious results (Table 1.3). Truncated models from E performed better when run on dissimilar A and C (Table 1.3, column 5). However, truncated models of D performed better when run on dissimilar A, but this was not the case when run on C, although the latter is also dissimilar. Similarly, the untruncated D model exhibited higher predictive-discriminative values when run on E, but vice-versa the truncated model had a slightly higher, albeit not very impressive (D_{XY} = 0.683), predictive-discriminative ability (Table 1.3). Models based on these data (D and E) did not, whether truncated or not, have acceptable values (i.e., > 0.6) of predictive-discriminative ability when run on the cross-over growth pattern (Table 1.3, columns 4 and 5).

1.6 Discussion

Truncating affected the values of predictor variables computed from live tree growth series (Fig. 1.1) and thus influenced the selection of variables in the models (Table 1.2). Consequently, truncating also affected parameter estimates (Table 1.2) and was therefore a data treatment with considerable impact on the modelling process of tree mortality probabilities.

The impact of truncating on a model's predictive-discriminative ability depended on the underlying growth patterns of the training and test data. In general, untruncated models had higher discriminative ability when applied to the same populations from which the models had been derived, or when the test (or application) population showed a similar growth pattern. In these cases, higher discriminative abilities stem from the fact that growing conditions have improved since dead individuals died, thereby leading to an increase in the growth levels of live trees. However, when such models were tested on data sets with dissimilar growth patterns, the truncated models were of better predictive-discriminative strength.

Logistic regression uses the difference between groups in the values of predictor variables to predict the probabilities of a binary outcome (e.g., live or dead status). The greater the difference in the predictor variable values, the higher the predictive-discriminative capacity of the resulting model. Here lies one of the reasons why growth trends (e.g. diverging vs. merging) determine the impact of truncating on the model performance. In situations of diverging chronologies, truncating tends to lower the difference in the predictor variable values computed for the live and dead tree populations. The procedure is thus expected to lower the predictive-discriminative strength of the model, whereas the opposite is true when chronologies show a merging trend.

Although a high predictive-discriminative strength is desirable when one wants to estimate mortality probabilities, the use of untruncated data in situations where external factors (e.g., disturbance, climate) may have had a potentially strong influence on the recent growth of trees gives this strength a somewhat artificial nature. This would not be the case for dead trees if many of them had already died before the onset of the external influence.

External factors such as disturbance or climate very often influence tree growth (Lorimer 1985, Nowacki and Abrams 1997) and this may lead to biased mortality models. The use of untruncated data will then confound climate or disturbance growth signals with tree vigor-related growth responses and will lead to high data specificity through the fitting of data-specific noise and thus to overfitted models (Harrell 2001). Truncating may alleviate this problem as is suggested by their superior external predictive-discriminative ability.

Our results suggest that truncating reduces the influence of external factors (e.g., disturbance, climate) on mortality probability estimations which translates into more accurate models with greater general applicability. Such a procedure is therefore expected to bring the model closer to its original intent, that is, to predict mortality probabilities from radial growth as a surrogate measure of tree vigor (Waring and Pitman 1985, Pedersen 1998a, 1998b). Whether our approach succeeds better in doing so than other approaches such as the explicit modelling of climate signal and intervention occurrences in growth series (Pedersen 1998b) has not been tested in our analyses and is beyond the scope of this paper. However, truncating has the advantage of being a simple method that does not rely on statistical assumptions and that is therefore not influenced by parameter estimation uncertainties.

If one uses growth variables to estimate mortality probabilities in trees, the general use of truncating is indicated. Truncating has shown to improve or, at worst, have little impact on model predictions. However, even lower predictive-discriminative strength in truncated models would promote truncating since these models more realistically reflect the underlying tree vigor relationships between live and dead trees.

The poor performance of the C models in discriminating tree status in other data sets, and the poor performance of other models in predicting C outcomes, highlights the need for cautious parameterization of mortality models. As indicated by the growth inversion following disturbance (Fig. 1.2B), vigorous and dominant trees were most severely affected by the disturbance agent which was, in this case, the spruce budworm (*Choristoneura fumiferana*) (C is data from balsam fir, the preferred host of the budworm). The subsequent decline and death of the overstory will enhance growth of suppressed and less vigorous trees. Since this species responds very well to release, even after extended periods of suppression (Frank 1990), and repetitively attacked overstory trees die in high proportions (Solomon et al.

2003), the disturbance caused a rapid shift in tree vigor from the dominant canopy trees to the lower strata. This prevented the typical negative growth trend to develop in declining trees and since some of the trees died even though they maintained high radial growth rates (Fig. 1.2B), neither growth trend nor growth level variables from the C are good predictors of mortality probabilities in other scenarios.

Tree size, where available, was used as a pairing factor to match live and dead trees to determine the year in which individual live series had to be truncated. Whilst this might be adequate in most situations, other potential confounding factors, such as tree vigor classes or crown position, could be useful in situations where, as in the C, vigorous, dominant trees show an abrupt decrease in growth before their death. In this instance, their dominant position may be closely linked to their decline (Batzer et Popp 1985).

Truncated models generally performed better than untruncated models when the growth pattern of the testing data was different. More data, spanning an even wider gradient of patterns would be necessary to conduct a more thorough analysis and to pinpoint the causes and extent of this behavior. Resampling procedures producing confidence intervals of the predictive-discriminative measures could facilitate this task through formal hypothesis testing but such procedures are currently unavailable (Harrell, F., personal communication). Also, simulated data might be helpful to further investigate the statistical behavior of truncated models under a variety of scenarios including multiple disturbances. Such investigations could be useful even for applications where tree mortality probabilities are estimated in a longitudinal ('on-time') approach (Bigler and Bugmann 2004b).

Overall, truncating has been shown to be an efficient data treatment in the context of mortality probability estimations. Although more studies may be necessary to further test the impact of truncating on model selection and performance and – in studies where probability estimations are the actual aim – on parameter estimations, it has been demonstrated that truncating can reduce the influence of external factors on the modelling process. When mortality algorithms are to be integrated in forest simulation models of general applicability, truncating will give the predictors (radial growth variables) more biological sense (Hawkes 2000) and could allow more process-(vigor-) oriented model parameterization which is an

important feature of mortality algorithms especially in a world of accelerated environmental change (Keane et al. 2001).

In simulation models (e.g. JABOWA, Botkin et al. 1972) where mortality occurs when growth becomes lower than a given threshold, and where model parameters (i.e., the threshold growth level in the case of mortality prediction) are derived from 'intelligent' guesses (Hawkes 2000), truncating does not apply since no empirical parameter estimation is undertaken. However, these models usually assume that mortality algorithm parameters are constant across species which is an unrealistic assumption (Kobe et al. 1995, Pacala et al. 1996, Wyckoff and Clark 2002). To counteract these shortcomings, a mortality algorithm has to be parameterized by comparing growth of live and dead trees (Wyckoff and Clark 2000) and in these situations truncating will make the parameter estimates more realistic.

However, we do not propose truncating as a means to develop a general mortality model spanning across species and geographic regions. Mortality probability models derived from field data are empirical in nature and remain dependent on parameterization. Still, this does not diminish the benefits of truncating: making a model as robust as possible where robustness is desired.

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II. USING LONGITUDINAL SURVIVAL PROBABILITIES TO TEST FIELD VIGOUR ESTIMATES IN SUGAR MAPLE

(*Acer saccharum* Marsh.)

Henrik Hartmann, Marilou Beaudet & Christian Messier

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2.1 Abstract

Tree mortality is a major force driving forest dynamics. To foresters, however, tree mortality is often considered a loss in productivity. To reduce tree mortality, silvicultural systems, such as selection cuts, aim at removing trees that are more likely to die. In order to identify trees with higher risks of mortality, field classifications are employed that assess vigour based on external characteristics of trees.

We used a novel longitudinal approach for estimating survival probabilities based on ring-width measurements, initially developed by Bigler and Bugmann (2004), to parameterize a survival probability model for sugar maple (*Acer saccharum* Marsh.) and to test whether field-assessed tree vigour classes are corroborated by survival probabilities determined from radial growth history. Data from 56 dead and 321 live sugar maples were collected in stands in western Quebec (Canada) that had undergone a selection cut ~10 years prior to sampling.

Our results showed that tree vigour established from external defects and pathological symptoms, using the classification of Boulet (2005), is partially corroborated by growth-driven survival probabilities. Moribund trees had lower survival probabilities than vigorous trees over several years in the period prior to vigour assessment. Intermediate vigour classes showed less obvious tendencies, but this may be due to the growth-independent nature of some defects used for their classification.

Although the timing of tree death may not be correctly predicted by the vigour classification (i.e., our results suggest that time of death generally was overestimated), its general agreement with survival probabilities determined from growth series make it a useful tool for tree selection in sugar maple stands under selection management.

Key words: Selection cut, radial growth, survival model, logistic model.

2.2 Résumé

La mortalité des arbres est une composante importante de la dynamique forestière. Toutefois, pour les forestiers la mortalité constitue souvent une perte de productivité. Afin de réduire cette perte, des traitements sylvicoles, telle la coupe de jardinage, visent à enlever les arbres susceptibles de mourir. Ainsi, pour identifier ces arbres en forêt, les forestiers utilisent des systèmes de classification de vigueur des arbres qui sont basés sur des caractéristiques externes (défauts) des arbres.

Nous avons recours à une nouvelle approche d'estimation de probabilité de survie, basée sur la croissance radiale des arbres et développée par Bigler & Bugmann (2004), pour paramétriser un modèle de probabilité de survie pour l'érable à sucre (*Acer saccharum* Marsh.). Nous utilisons ces probabilités longitudinales de survie comme estimée de la vigueur des arbres et nous les comparons avec les estimées de vigueur obtenues en forêt. Nous avons échantillonné 56 arbres morts et 321 arbres vivants dans des peuplements d'érables au Québec occidental (Canada). Ces peuplements avaient subi une coupe de jardinage ~ 10 ans avant l'échantillonnage.

Nos résultats montrent que le système de classification sous étude (Boulet 2005) et les probabilités de survie donnent des estimées de vigueur similaires pour les classes extrêmes (arbres moribonds et arbres vigoureux). Les arbres moribonds avaient des probabilités de survie inférieures aux arbres vigoureux pour plusieurs années avant l'échantillonnage. Toutefois, le classes de vigueur intermédiaires du système de classification de terrain ne coïncident pas nettement avec les probabilités de survie ce qui semble être dû à la nature des critères d'évaluation sur le terrain.

Quoique le système de classification de vigueur testé dans cette étude ne peut pas prédire l'incidence de la mort des arbres correctement (le temps jusqu'à la mort est sous-estimé), sa concordance générale avec les probabilité de survie lui accorde un potentiel intéressant comme outil pour la sélection d'arbres dans les érablières sous aménagement jardinatoire.

Mots clés: Coupe de jardinage, croissance radiale, modèle de probabilité de survie, modèle logistique.

2.3 Introduction

Tree mortality is a major force driving forest dynamics and succession (Franklin et al. 1987, Pacala et al. 1996). It influences species composition, together with the size and age-structure of forest stands (Oliver and Larson 1996), and is a key process in nutrient and biomass cycling (Brown and Schroeder 1999). Knowledge of mortality rates is necessary for developing sustainable forest management practices (Davis et al. 2001). However, our understanding of the processes underlying tree mortality remains limited and warrants further investigation (Manion and Lachance 1992, Hawkes 2000).

In young stands undergoing canopy closure, trees die through self-thinning when increasing population densities limit resources for particular individuals (Yoda et al. 1963). Suppressed trees decrease their growth rates, which in turn reduces their competitive capacity under conditions of limited resources (Oliver and Larson 1996). In mature stands, tree mortality rates may be indicators of environmental stresses (Brooks 1994, Pedersen 1999, Dobbertin 2005), such as insect defoliation or drought, which may weaken individual trees until they die (Manion 1981).

In forest management, tree mortality is often seen as a loss in forest productivity, and standing dead trees (snags) are considered a potential danger during logging operations, although more recently their ecological role has been recognized (e.g., DellaSala et al. 1995, Hunter 1999). Nevertheless, most partial harvests, such as the selection system, attempt to remove low-vigour trees (Smith et al. 1997), thereby reducing future mortality losses while liberating resources for the residual trees. The residual stand therefore is expected to have a higher proportion of 'healthy' trees than before harvest, and to offer better growth conditions for residual trees, which should translate into lower mortality rates. However, to achieve this goal of decreasing post-harvest stand-level mortality rates, individual-level tree vigour must be adequately assessed in the field prior to harvesting under operational conditions.

Several tree classification systems have been developed to assess tree vigour based on social, morphological and pathological qualities of the target trees (e.g., Ouellet and Zarnovican 1988), crown characteristics (Millers et al. 1991) or bark characteristics (OMNR 2004). Although these indicators may be adequate tools for tree selection, their use may have

unintended consequences. For example, it has been observed that stands under industrial management had mortality rates five years after selection harvest that were higher than expected, based on previous experimental studies (Bédard and Brassard 2002). These higher-than-expected mortality rates, which occurred among trees without obvious harvest damage (skidding wounds, crown damage from felling, etc.), might be a consequence of ambiguous or ineffective marking guidelines (Meunier et al. 2002) that rely on visual assessments of tree vigour. If inadequate criteria are used, low-vigour trees may be retained to in harvested stands. However, the link between tree classification and future mortality occurrence has not been empirically tested.

Other approaches for assessing tree vigour are based on measures of photosynthesis, gas exchange or nutrient content in leaves, transport rates of water or ions, as well as measurements of tree vital function such as radial growth (Gehrig 2004). Radial growth of tree stems is assumed to be a low priority in carbon allocation; it varies with growth conditions (e.g., soil, climate, and competition) and has been used as a sensitive surrogate measure of the carbon balance of trees (Kobe et al. 1995, Kobe 1997). It is also a potentially useful indicator of stress and tree vigour (Waring and Pitman 1985, Pedersen 1998). Radial growth increment has been used to assess survival probabilities of individual trees by comparing growth of live and dead trees (e.g., Monserud 1976, Hamilton 1986) and is considered a viable approach to assess tree vigour.

To date, most studies of tree mortality probabilities are based on a cross-sectional approach where the data consist of a single measurement of recent growth per tree. These data can take the form, for example, of the ring-width or basal area increment in the year prior to sampling or prior to the year of death, or some derived variable such as the mean growth rate over a given period of recent growth (e.g., Bigler and Bugmann 2003). With this approach, predictions of tree status (dead or alive) are accurate only at one single point in time, namely, the year when growth measurements are taken or the period for which the predictor variable was computed. Therefore, the cross-sectional approach cannot be used to predict mortality probabilities for other periods in a tree's life. More recent studies have used a longitudinal approach to model the probability of mortality over time, for example, for the entire life span of trees (Bigler and Bugmann 2004, Bigler et al. 2004).

Unfortunately, radial increment cannot be easily measured in the field, since it requires repeated diameter measurements or increment core sampling. This repeated measurement precludes its use as a tool for vigour assessment and tree selection on an operational basis. However, radial growth can provide a powerful validation of existing vigour classifications by comparing survival probabilities of trees of different vigour classes (Bigler et al. 2004).

In this study, radial growth rates of sugar maple (*Acer saccharum* Marsh.) were used to parameterize a survival probability model for empirically estimating tree vigour. These survival probabilities were compared to field estimations of tree vigour using the classification system described in Boulet (2005). Sugar maple was selected for our study because it is a major, ecologically important North American tree species. It is shade tolerant and forms uneven-aged stands of great geographical extent spanning the northeastern USA and eastern Canada (Godman et al. 1990).

The objectives of this study were to: (1) develop a longitudinal survival probability model using radial growth series from sugar maple trees from stands in western Quebec, Canada, and (2) use this model to determine whether survival probabilities corroborate the visual classification of tree vigour used for tree marking.

2.4 Material & methods

STUDY AREA

The study sites are located in the Abitibi-Temiscamingue region of western Quebec, about 60 km southeast of the city of Temiscaming (46°43' north, 79°04' west). The region is part of the western sugar maple-yellow birch bioclimatic domain (Robitaille and Saucier 1998). Mean annual temperature varies from 2.5 to 5.0°C; growing season extent is 170 to 180 days, and mean annual precipitation ranges from 800 to 1000 mm, with about 25% of total precipitation falling as snow (Gosselin et al. 2000). Soils are derived principally from glacial till, with the remainder originating from fluvio-glacial deposits in the large valley bottoms, and peat-bogs in poorly drained depressions (Robitaille and Saucier 1998).

In 2004 and 2005, 19 plots (26 m x 56 m) were established in uneven-aged sugar maple stands that had been harvested by selection cuts in 1993 or 1994. The studied stands had an average pre-harvest basal area of 27 m^2/ha, which was reduced by harvesting to an average 21 m^2/ha. On average, maximum canopy height reached 25-28 m. The entire area experienced two forest tent caterpillar (*Malacosoma disstria* Hubner) outbreaks (1971 and 1988), which caused heavy defoliation in sugar maple (MRNFP 2002, MRNF 2005), one of its host species (Fitzgerald 1995).

In our plots, sugar maple made up 68% of total basal area, yellow birch (*Betula alleghaniensis* Britton) about 18%, red oak (*Quercus rubra* L.) 3.5%, and American beech (*Fagus grandifolia* Ehrh.), eastern white cedar (*Thuja occidentalis* L.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.) each constituting roughly 1.5% of the total. Other species such as balsam fir (*Abies balsamea* [L.] P. Mill.), white spruce (*Picea glauca* [Moench] Voss), and red maple (*Acer rubrum* L.) occurred in minor proportions (< 1% of total basal area).

Plots were established at locations where site characteristics were considered representative of the greater region, i.e., on level ground or on gentle slopes with good to moderate drainage, and on podzols of glacial origin. In these plots the diameter at breast height (*dbh*, 1.3 m above ground level) and crown class (dominant, codominant, intermediate, suppressed) of all trees >10.0 cm *dbh* was determined. Also, tree vigour was assessed using a visual classification system (see below) and three increment cores for each live tree between

19.1 cm and 49.0 cm *dbh* were taken as a retrospective measure of radial stem growth. Trees <19.1cm and >49.0cm were excluded from sampling to avoid heavily suppressed or senescent individuals.

TREE VIGOUR CLASSIFICATION

The tree vigour classification that we used has been developed by the Quebec Ministry of Natural Resources (Boulet 2005), and relies on pathological symptoms (e.g., presence of cankers and fungi), mechanical damage (e.g., cracks, leaning) and other visible features (e.g., improper branch shedding, crown openness) to assign trees to 200+ vigour codes, which are then grouped into four main vigour classes. The classification system is considered a thorough framework for tree vigour assessment and, since it is based on symptoms of physiological vigour decline, can be regarded as an indicator of tree vigour beyond the geographical boundaries of where it was developed. The vigour classification takes into account wood properties, but also assigns tree survival probabilities until the next harvest entry, typically scheduled every 20-25 years (MRN 1997).

The four vigour classes are described as follows. Trees of reserve stock (class 'R') are free of any symptoms of disease or damage and are considered 'healthy' trees with the highest probability of survival. Growing trees (class 'C') have minor defects but are not biologically declining and are expected to survive until the next harvest without risk of imminent wood decay. Low quality or defective trees (class 'S') are considered to be declining in terms of vigour, wood quality and volume increment, and are not expected to survive until the next harvest. Moribund trees (class 'M') show signs of either lethal pathological infection or severe damage with high risk of trunk breakage. Moribund trees are biologically declining (decreasing vigour, wood decay) and are assumed to have a high probability of mortality before the next harvest entry.

The vigour classification system has a hierarchical structure based on the assumed severity of observed defects. When assessing a tree's vigour, one should first determine whether the tree shows signs or symptoms of fungal infection (sporocarps, stroma) and, if present, this observation determines the vigour code. If the tree is free of fungal infection, then signs or symptoms of cambium necroses (cambial diseases) should be determined and, if

present, they will determine the vigour code. The stepwise assessment procedure continues further using various types of criteria, in the following order: bole defects and bark mechanical injuries, root and butt wounds, bark fissures and bole cracks, woodworm and woodpecker damage (wood dust and bird-pecks), crown defects, and finally, branching defects.

Listing all possible defects for vigour classification is beyond the scope of this paper. However, typical fungal infections for sugar maple involve the northern tooth fungus (*Climacodon septentrionalis* [Fr.] P. Karst.), which causes severe crown dieback. In all cases, sugar maples showing signs of this fungal infection are classified as moribund. However, the mere presence of a pathogen does not automatically relegate the infected tree to moribund status. For example, latent stump decay incurred by the mossy maple conk (*Oxyporus populinus* [Schumach.] Donk, [1933]) only leads to a 'C' code if present at or below 60 cm from the base of the stump. If the same pathogen is encountered higher on the trunk and is associated with necroses, cracks, and heart rot, the tree would be given an 'M' code. Similar complex ratings apply to necroses. For example, the presence of cankers such as *Neonectria* sp., *Eutypella* sp., or *Sirococcus* sp. would rate a 'C' code, if no or only superficial wood decay is visible. If heart wood decay (> 5 cm in depth) is present but the necroses covers less than one apparent side of the trunk, the associated code is 'S.' However, if the necrosis spans over more than one apparent side of the trunk, the tree is then classified as moribund.

Other classification criteria, such as trunk deformations, bark cracks, and root or crown damage are more straightforward to identify than pathogen infections, but their inclusion adds to overall classification complexity as well. More details of the rating system can be found in the field guide (Boulet 2005).

TREE GROWTH DATA

While all growth data for live trees were obtained from increment cores taken from trees inside the study plots, the number of dead trees in the plots was insufficient for our analyses. We therefore had to extensively search for dead trees throughout the entire area of the 1993 and 1994 harvest blocks. However, we only sampled dead trees that were on sites and within stands similar to those where the initial live tree plots were located. Also, only trees with

evidence of recent death (1993 or later) were selected, based on the presence of bark and fine branches, and on the absence of advanced trunk decay (Sénécal et al. 2003).

Dead tree growth data for parameterizing the survival probability model (see below) were collected from dead trees without any evidence of obvious causes of instantaneous death (uprooting, bole breakage, etc.). This was to exclude growth-independent factors from influencing the parameter estimates of the growth-driven survival probability model. Standing dead trees were felled and a cross section of the trunk at 1.3 m above ground level was sampled.

A total of 321 live and 56 dead trees were sampled, with a more or less uniform distribution among *dbh* classes (19.1-29.0 cm, 29.1-39.0 cm, 39.1-49.0 cm). Increment cores and cross sections were progressively sanded down to grain 400 to allow a clear identification of the final cell layer in each tree-ring. Tree-rings were measured using a microscope equipped with a computer-assisted micrometer (0.001 mm precision). Of the three increment cores taken per live tree, at least two were readable in most cases, and were used for growth measurements. For the dead trees, two radii per tree were chosen from cross sections so that growth measurements could be undertaken. These tree-level measurements were averaged to account for intra-tree variability of radial increment due to growing conditions or leaning (Kienholz 1930, Peterson and Peterson 1995).

A subsample of dominant live trees was selected to construct a master chronology using the program COFECHA (version 6.06P, Holmes 1983). Live and dead tree-ring series were then cross-dated based on the visual examination of marker years and correlation with the master chronology. All tree-ring series showed a severe growth decline in 1988 and this decline served as reliable marker year. After a visual dating with these marker years, COFECHA was used to detect missing or false rings in individual tree-ring series, which were then identified on the cores or cross sections. These missing or false rings were then added or removed from the series and COFECHA was run again to verify the cross-correlation with the master chronology. This procedure was repeated until good cross-correlations ($r \geq 0.3$, Tardif et al. 2001) with the master chronology were obtained. For live trees, the series covered calendar years from 1878 (healthy) or 1898 (moribund) to the year of sampling (2004), whereas the dead tree series (measured completely from cross sections)

covered calendar years 1848 to 2003 or earlier, depending on the year of death of individual trees.

From the 321 live trees sampled in our plots, 56 individuals (i.e., a number equivalent to the sample size of dead trees) were randomly selected and used to parameterize the survival probability model. To assure that growth of selected trees (and the resulting survival probability model) had not been negatively influenced by direct harvest disturbance, live trees were selected only when our field assessment indicated absence of obvious harvest disturbance (i.e., trees not close to skid trails and not heavily thinned).

LOGISTIC REGRESSION

Logistic regression was used to model survival probabilities as a function of radial growth, in the following form (Bigler and Bugmann 2003):

[eq. 1] $$P(Y = 1) = \frac{e^{\beta X}}{1 + e^{\beta X}}$$

where $P(Y = 1)$ is the probability that an individual tree survives given the matrix of independent variables X. The latter include three types of growth variables: (i) growth level (average growth over a specified period), (ii) growth trend (regression slopes of growth over a specified period) and (iii) growth sensitivity (average growth variability over the preceding 5 years, see below for details). The vector β of regression parameters is estimated in the analysis (Hosmer and Lemeshow 2000, Quinn and Keough 2002).

A manual stepwise procedure was used in the modelling process. First, only one growth level variable was included at a time. The growth level predictor variables that we considered were the log-transforms of the arithmetic mean over the preceding 3, 5 and 10 years of radial growth (Table 2.1). The log-transformation was applied to lower the weight of very high growth values. Using the Akaike Information Criterion (AIC, Burnham and Anderson 2002), the D_{XY} and bootstrapped confidence intervals (see below) were used as the main decision criteria for selecting the 'best' univariate model, which was then used for further analysis. Second, growth trend variables were added individually to the best univariate model. The

growth trend variables that we considered were the coefficients of the local linear regression over the preceding 3, 5, 10, and 25 years (Table 2.1).

Table 2.1
Growth level, growth trend and growth sensitivity variables computed for different time windows used for logistic regression analysis of survival probabilities. Shown are variable names and their respective number of observations, including live and dead measurements. Number of observations of dead measurements are constant across growth variables and equal the number of dead trees (n=56)

	Types of growth variables					
	Level*		Trend		Sensitivity	
No. of tree-rings to compute variable	Variable name	n	Variable name	n	Variable name	n
1	rw-log	9727	.	.		
3	av3-log	9722	slp3	9727		
5	av5-log	9512	slp5	9504	sens5	9727
10	av10-log	9286	slp10	9283		
25	.	.	slp25	8723	.	.

* log transformed

To avoid redundancy, only one growth trend and one growth level variable was allowed in the final model. Last, the mean sensitivity over the preceding 5 years was added to the best bivariate model. This variable represents the responsiveness of individuals to environmental signals, such as climate (Fritts 1976). High sensitivity values have been associated with tree vigour decline because dying trees may exhibit higher variability in past growth rates (Ogle et al. 2000, Suarez et al. 2004). Interannual sensitivity was defined as (Fritts 1976):

[eq. 2] $$S_t = \frac{abs(rw_t - rw_{t-1})}{abs(rw_t + rw_{t-1})}$$

where S_t is the sensitivity in the year t, and rw is the ring width measurement in the year t. We used the average sensitivity of the most recent 5 years, assuming that declining trees would exhibit growth variability during the period close to their death.

Parameter estimation was done with R software (version 2.4.0, R Development Core Team 2006), using maximum log-likelihood. The model with the lowest AIC was retained for further analysis. Non-parametric confidence intervals for parameter estimates were computed using a bootstrap resampling procedure (*bootcov*) with 1000 repetitions and applying the 25th

and the 975th quantile as interval limits. Longitudinal data from tree-rings are interannually correlated and, therefore, are not independent within an individual tree-ring series. This violation of independence will underestimate the true variance and confidence interval width. To correct for within-cluster (i.e., within-tree) correlation of the responses, the *bootcov* function was used, which allows substituting cluster sampling with replacement for the usual simple sampling with replacement. The resulting parameter estimates therefore can be regarded as unbiased and were considered significant when the confidence interval did not include zero; otherwise the model was rejected even if it had a lower AIC.

To obtain additional information on the gain in model performance when variables were added, Somer's D_{XY} index was used as another decision criterion (Somers 1962). D_{XY} is indicative of the model's discriminative ability and is closely related to the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Engelmann et al. 2003) and, as such, is independent of prevalence and classification thresholds (Swets 1988). It ranges from -1 (indicating perfect status misclassification, where all live trees are classified as dead or vice-versa) to 1 (perfect status classification); values >0.6 indicate good discrimination (see Manel et al. 1999). To account for over-optimistic classification measures when validating the model on the training data (data specificity), the bootstrap resampling procedure *validate.lrm* from the *R Design* library (Harrell 2005) was used. This procedure eliminates the optimism of the D_{XY} due to overfitting and produces a more conservative estimate of the model's discriminative ability (Harrell 2001).

LONGITUDINAL SURVIVAL PROBABILITY ESTIMATIONS

Survival probabilities were estimated following a longitudinal approach to logistic regression developed by Bigler and Bugmann (2004). This method uses tree-ring data from live and dead trees to estimate survival probabilities over the life span of a tree. To do so, growth data from the entire life span of the trees must enter the modelling process. First, tree growth variables (e.g., mean values and trend coefficients over different periods) are computed as predictor variables. Variables containing the last year of growth of a dead individual are marked as 'dead' measurements. All measurements of dead trees, excluding those from the year of death, and all live tree-ring measurements are marked as 'live'

measurements. The logistic regression model is then fitted to data points from the entire life span of all trees.

COMPARISONS OF SURVIVAL PROBABILITIES

Among the available tree growth series (321 live, 56 dead), the data were divided into five distinct groups according to the status (live or dead) and vigour code of live trees. Individual survival probabilities were computed for vigorous ('R', n = 160), growing ('C', n = 87), declining ('S', n = 31), moribund ('M', n = 43) and dead ('D', n = 56) trees, and compared among groups. A series of annual ANOVAs was applied to determine whether within-year differences in survival probabilities varied statistically (P <0.05) among these five groups. For years with significant differences, Tukey's HSD adjustment for multiple comparisons was applied to obtain adjusted P-values for unplanned comparisons between pairs of groups (Quinn and McKeough 2002).

2.5 Results

In the first step of the regression analysis, the univariate model with the best fit (lowest AIC) contained the log-transformed averages over the last 3 years of growth (model 2, Table 2.2). Although the log-transformed annual measurement (rw-log, model 1) yielded a model with a higher D_{XY} (0.772) than model 2 (0.715), its AIC was markedly higher (587.1) than that of model 2 (545.9, Table 2.2). The addition of the growth trend variable yielded bivariate models with consistently lower AICs than univariate models. However, the inclusion of 10-year slopes and 25-year slopes decreased the D_{XY} to 0.707 and 0.710, respectively (Table 2.2). Among the two models with lower AICs and higher D_{XY} values, the addition of the trend over 5 years yielded an AIC (513.5) well below the model including the 3-year slope (519.5, Table 2.2). Therefore model 6 (D_{XY}=0.783) was considered for further analysis even if the D_{XY} was slightly greater for model 5 (0.798). The addition of the sensitivity variable to this model caused a slight decrease in the AIC (510.0) and little improvement in the D_{XY} (0.793), but the confidence interval of the parameter estimate spanned across zero, so this predictor was rejected as being significant (Table 2.2).

Table 2.2
Parameter estimates, bootstrapped 95% confidence intervals (CI), AIC, and optimism-corrected D_{XY} of logistic mortality models. Models in bold are the 'best' univariate or bivariate models

Independent variables		Estimate	CI (95%) Lower	CI (95%) Upper	AIC	D_{XY}
Univariate models						
Model 1	Intercept	-1.740	-5.379	0.053	587.1	0.772
	rw-log	1.093	0.799	1.721		
Model 2	**Intercept**	**-6.589**	**-8.422**	**-4.724**	**545.9**	**0.715**
	av3-log	**1.872**	**1.567**	**2.193**		
Model 3	Intercept	-7.088	-9.397	-4.424	567.1	0.634
	av5-log	1.923	1.476	2.335		
Model 4	Intercept	-8.153	-11.121	-4.974	586.3	0.563
	av10-log	2.052	1.547	2.551		
Bivariate models						
Model 5	Intercept	-7.623	-9.555	-5.792	519.5	0.798
	av3-log	2.082	1.779	2.440		
	slp3	0.004	0.002	0.005		
Model 6	**Intercept**	**-7.115**	**-8.974**	**-5.337**	**513.5**	**0.783**
	av3-log	**2.017**	**1.713**	**2.375**		
	slp5	**0.006**	**0.004**	**0.007**		
Model 7	Intercept	-6.278	-8.393	-4.242	540.9	0.707
	av3-log	1.826	1.493	2.202		
	slp10	0.003	-0.005	0.008		
Model 8	Intercept	-5.820	-7.943	-4.018	534.4	0.710
	av3-log	1.756	1.455	2.132		
	slp25	0.008	-0.007	0.017		
Trivariate model						
Model 9	Intercept	-5.951	-8.414	-3.508	510.0	0.793
	av3-log	1.904	1.536	2.302		
	slp5	0.005	0.003	0.007		
	sens5yr	-2.622	-5.154	0.420		

Means of the growth level variable were similar among the intermediate vigour classes, which in turn differed significantly ($P < 0.001$) from the means for vigour class R and the dead trees (Table 2.3). Mean log-transformed growth over three years (av3-log) of live trees varied between 6.893 (vigour class M) and 6.999 (R) but was only 6.742 for dead trees (Table 2.3). Slopes over 5 years showed a direct relationship with vigour; mean regression slopes decreased with vigour and ranged from positive (5.654, R) to negative values (-4.956,

M, Table 2.3). However, slopes were statistically different only between vigour class R and M (P <0.05) and vigour class R and D (P <0.001). Interestingly, regression slopes of moribund and dead trees (-4.570) were quite similar (Table 2.3).

Table 2.3
Sample sizes (n), mean values and standard errors (SE) of the predictor variables av3-log [ln(3-year average growth(μm/yr)+1)] and slp5 [5-year regression slope (μm/yr)] of live trees in different vigour classes and dead trees

			Predictors			
			av3-log		slp5	
	Vigour class	n	Mean	SE	Mean	SE
Live	R	160	6.999^{A}	0.627	5.654^{a}	183.167
	C	87	6.920^{B}	0.657	2.170^{ad}	177.333
	S	31	6.918^{B}	0.698	2.651^{ad}	183.857
	M	43	6.893^{B}	0.645	-4.956^{bd}	201.980
Dead	D	56	6.742^{C}	0.679	-4.570^{Cd}	142.456

Upper case letters, if different between vigour classes, indicate a significant difference at P <0.001, lower case at P <0.05, Tukey's HSD.

More than 80% of vigorous trees had no defects, while the reminder had cracks (5.0%), bole (4.4%), root and butt defects (3.8%), or bird pecks and branching defects (both 3.1%, Table 2.4). These defective trees showed no signs of decay. Most defects of growing trees were bole cracks lacking signs of decay or bird pecks, which together affected more than 75% of trees in this class (Table 2.4). Declining trees were mostly affected by bole defects (25.8%), bird pecks (22.6%) and cambium necroses (19.4%). There was evidence of fungal infection in one individual in this class (Table 2.4). Moribund trees were mostly affected by sporocarps and stromata (26.6%), together with cambium necroses (52.4%) and decayed cracks (14.3%), which characterized more than 90% of trees in this class (Table 2.4).

Table 2.4
Number of trees per defect type and their respective percentage distribution within each vigour class

	Vigour class							
	R (vigorous)		C (growing)		S (declining)		M (moribund)	
Defect	N	%	N	%		%	N	%
None	129	80.6	0	0.0	0	0.0	0	0.0
Sporocarps	0	0.0	3	3.4	1	3.2	11	25.6
Necroses	0	0.0	0	0.0	6	19.4	23	53.5
Bole	7	4.4	8	9.2	8	25.8	1	2.3
Root&butt	6	3.8	3	3.4	0	0.0	1	2.3
Cracks	8	5.0	36	41.4	4	12.9	6	14.0
Bird pecks	5	3.1	31	35.6	7	22.6	1	2.3
Crown	0	0.0	2	2.3	1	3.2	0	0.0
Branching	5	3.1	4	4.6	4	12.9	0	0.0
Total	160	100.0	87	100	31	100	43	100

For all vigour classes, there was a strong growth decline apparently due to disturbance in 1971 and 1988 (Fig. 2.1a). Average annual growth rates of vigorous trees (R) were consistently higher than growth rates of trees in other vigour classes, at least from the 1960's onwards, but showed a similar pattern (Fig. 2.1a). On the other hand, growth of dead trees (D) showed a distinct pattern of steady decline from 1960 onwards, with a small increase in the last year (Fig. 2.1a). This apparent recovery is likely due to the continued decrease in sample size of dead trees (Fig 2.1b) and associated higher variability in dead tree data towards the end of the series (Fig. 2.1c).

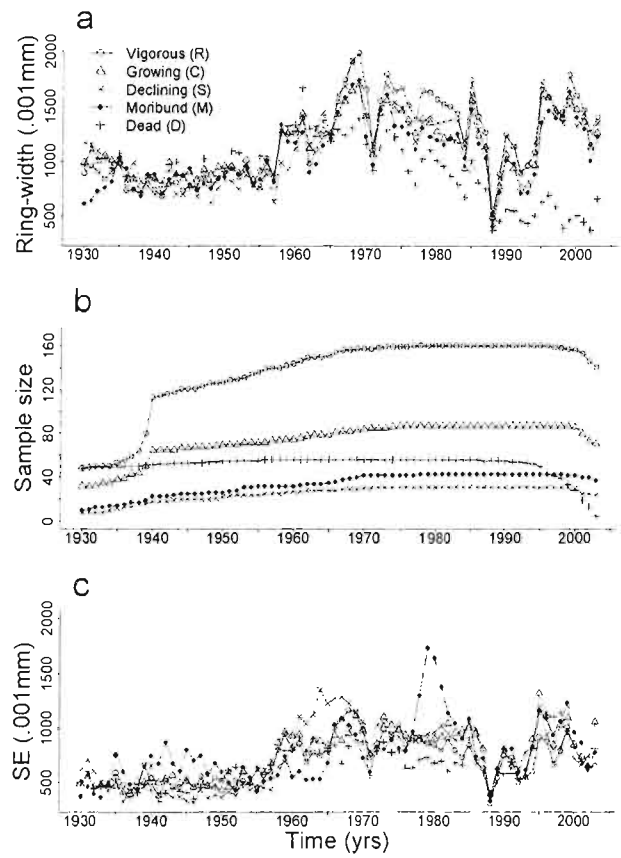

Figure 2.1 Median annual ring-width (a), sample sizes (b), and standard errors (SE) of means (c) from 1930 to 2003 for vigorous (R), growing (C), declining (S), moribund (M) and dead (D) adult sugar maple trees. Ring-widths were measured to 0.001 mm precision. Note the strong decline in sample size of dead trees due to mortality related drop-out.

Survival probabilities were compared from 1970 onwards for more than 30 years prior to vigour estimation. Survival probabilities of dead trees were statistically different (P <0.05) from those of live trees (all vigour classes) in 1976 through 1978, 1985, and in every year from 1987 until 2003 (Fig. 2.2a). Differences among vigour classes were less apparent and did not cover longer periods (Fig. 2.2b). In the late 1970's survival probabilities of declining trees were significantly lower than those of vigorous (1976, 1977, and 1978) and growing (1977) trees (Fig. 2.2b). In 1989, which was the year following defoliation, survival probabilities dropped as markedly as radial growth in 1988 (Fig. 2.1a) but similarly among

vigour classes. Another decline occurred in 1993-1994, the years when harvesting took place, but this trend was followed by a quick recovery (Fig. 2.2b).

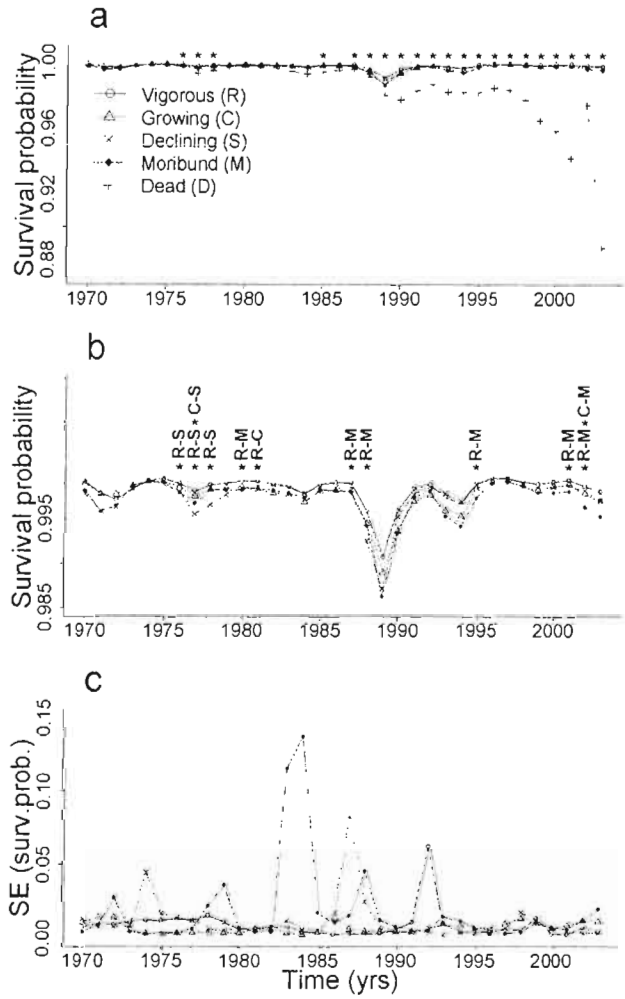

Figure 2.2 Survival probabilities (a, b) and their standard errors (c) from 1970 to 2003. Panel a shows survival probabilities of vigorous (R), growing (C), declining (S), moribund (M), and dead (D) trees; panel b excludes dead trees. Asterisks (*) above the curves in (a) indicate the years of significant differences ($P < 0.05$, ANOVA) between dead and live (all vigour classes), in (b) asterisks indicate the years of significant differences ($P < 0.05$) between vigour classes based on Tukey's HSD tests for years with significant ($P < 0.05$) annual ANOVAs. Vigour classes that were significantly different from each other are listed in panel (b), with a dash separating significantly different groups.

Survival probabilities of vigorous trees were significantly higher than those of moribund trees in 1980, 1987, 1988, 1995, 2001, and 2002, and higher than those of growing trees in 1981 (Fig. 2.2b). Also in 2002, survival probabilities of growing trees were higher than those of moribund trees (Fig. 2.2b). Standard errors of the means were large for moribund (1983-1984, 1988), declining (1987) and vigorous (1992) trees, but low for most of the time before and especially after these brief periods (Fig. 2.2c).

2.6 Discussion

LINKING FIELD VIGOUR ESTIMATES TO RETROSPECTIVE SURVIVAL PROBABILITIES

We used radial tree-ring series to estimate retrospectively survival probabilities for the entire life span of trees and used these probabilities to test the validity of a field vigour classification system. Whilst the former methodology has been proven adequate (Bigler and Bugmann 2004), the latter is more ambiguous especially if vigour was estimated at the very end of the tree-ring series. It is obvious that tracing back vigour estimates through time is challenging. At what point in time has a tree entered a vigour class estimated in 2004 and how did this influence radial growth rates?

Trees that were showing signs or symptoms of advanced lethal pathogen infection in 2004 (e.g., presence of perennial conks) had been already under attack for some time, in the case of the tinder fungus (*Fomes fomentarius* [L.] J.J. Kickx) up to 30 or more years (Schmidt 2006). Also, it has been observed that pine trees (*Pinus mugo* Turra) were infected and killed by *Armillaria* spp only if they were weakened by competition and this weakening translated into a gradual, several decades lasting decline of radial growth prior to death (Cherubini et al. 2002). These low growth rates were estimated as preconditioning to fungal attack and not as its result (Cherubini et al. 2002). Similarly, Pedersen (1998) found that oak trees (*Quercus* spp) died several decades after an inciting drought stress and that these trees had lower growth rates than surviving trees during this period. Lower growth rates of dead trees prior to drought were considered indicative of the preconditioning of these trees to further decline (Pedersen 1998). On the other hand, Davis et al. (1997) observed that heavily cankered (*Cryphonectria parasitica* [Murrill] Barr) scarlet oak trees (*Quercus coccinea* Münchh.) had higher growth rates (basal area increment) than moderately cankered individuals, but their growth rates were still lower than non-cankered trees. Potential mechanisms for this growth stimulation were attributed to callus formation close to the sites of infection and sampling, and thus, were considered worthy of further investigation (Davis et al. 1997). Whether or not slow growth rates are the cause or the consequence of fungal infection may still be an open question, but both phenomena often coincide. Also, declines due to fungal infection or other sources of stress are slow processes, which may last decades. Signs (sporocarps, stromata, cankers) or symptoms (wood decay, crown dieback) of fungal

infection therefore can be assumed to be reliable criteria for estimating tree vigour in the field and can be linked to survival probabilities estimated from past radial growth rates.

Similarly, severe crown dieback, if chronic or induced by competition or drought, classifies a tree as moribund when >26% of the crown is dead in suppressed individuals and >51% of the canopy of trees with open, chlorotic and dwarf-leaved crowns is dead (Boulet 2005). Although severe crown dieback (i.e., >40%) cannot not be supported by trees for very long periods (Gross 1991), our data show (Fig. 2.1a) that a single severe crown defoliation caused by a forest tent caterpillar outbreak (1971) initiated severe declines in growth rates that persisted over decades in less vigorous trees. Similar results have been observed in trembling aspen (*Populus tremuloides* Michx.) where crown defoliations reduced radial growth rates and predisposed trees to attack by wood-boring insects and fungal pathogens (Hogg et al. 2002).

Structural defects, such as butt defects, bole cracks or strong leaning, reduce survival probabilities by increasing the risk of mechanical failure. The presence of deep cracks decreases the tree's mechanical resistance to external forces, such as wind, and increases the tree's risk to fall over (Smiley et al. 2007). These risks are unlikely to show in radial growth rates but the vigour classification system assigns a moribund code only to major structural defects (e.g., crack >1.5 m) that are accompanied by profound wood decay caused by fungal activity (Boulet 2005). However, because fungal infections in this instance are a result of mechanical damage rather than one of reduced vigour, their linkage to radial growth rates may be difficult to detect. This decreases the potential of survival probabilities inferred from radial growth to reflect vigour classification in these cases.

VALIDATING THE FIELD VIGOUR ESTIMATES WITH GROWTH-DEPENDENT SURVIVAL PROBABILITIES

In this study, radial growth of dead and, to a lesser extent, moribund trees diverged from that of vigorous trees shortly after 1971 and onwards (Fig.2.1a). This and a subsequent growth decline in 1988 can be linked to forest tent caterpillar defoliation, a disturbance recurring over about a 9-year cycle in the study region (MRNFP 2002, MRNF 2005). A comparison of growth rates in sugar maple (a host species) and yellow birch (a non-host

species) clearly showed that birch did not incur the same growth reduction as sugar maple (H. Hartmann, unpublished data), supporting the hypothesis that the growth decrease observed among maples resulted from tent caterpillar defoliation and not from other disturbances (e.g., drought). Growth declines prior to death are consistent with Manion's tree decline model (Manion 1981), where predisposing stresses reduce tree vigour and inciting factors cause a final decline and death. For dying trees, the first defoliation (although not a long-term stress, as stated in Manion's model) reduced tree vigour, i.e., growth rates and survival probabilities, and predisposed these trees to a second, more intense forest tent caterpillar defoliation, which led to an accelerated growth decline and to death (Fig. 2.1a). Average growth rates during these defoliations were (although not significantly) higher in vigorous than in moribund trees, possibly indicating that their greater carbon reserves allowed for quick foliage replacement and growth recovery (McLaughlin et al. 1980).

Survival probabilities corroborate, at least partially, the visual tree vigour classification used for tree marking. The different vigour classes that are used in Quebec (Boulet 2005) are supposed to broadly predict tree survival probabilities. It is assumed that moribund trees will likely die before the next harvest (over the next 20 to 35 years), whereas declining trees should survive until the next harvest despite their decreasing vigour (and hence, survival probability). Growing and vigorous trees are assumed to have unconstrained life expectancy.

Although the average 5-year slope of moribund and now dead trees was negative (Table 2.3), survival probabilities of moribund trees showed no monotonic negative growth trend over the most recent 30 years (Fig. 2.2a), as has been observed in other studies (Bigler et al. 2004). This may be due to the fact that, in this study, vigour estimates were based on external signs and symptoms related to vigour but not on any actual measures of physiological activity. Bigler et al. (2004, p.185) used cambial vitality, a measure that "correlated significantly with the number of cells produced by the cambium", for vigour estimations in European silver fir (*Abies alba* Mill.). Obviously, the number of cells produced by the cambium correlates well with tree-ring width. However, vigorous, growing and declining trees in this study had higher (positive) average growth trends computed over the entire tree-ring series than those of moribund and dead trees (negative, Table 2.3), indicating that moribund and now dead trees showed an overall growth decline over their life span.

In this study, mean survival probabilities of vigorous trees were greater than those of moribund or declining trees for most years from 1970 onwards, although not consistently throughout this period (Fig. 2.2a). The growth-driven survival probability model used in this study may not correctly predict survival probabilities in trees affected by growth-independent defects, such as bole cracks, which accounted for roughly 14% of moribund trees. Similarly, most growing (≈90%) and declining (≈61%) trees were classified based on bole injuries, root butt defects, cracks or bird pecks (Table 2.4). None of these defects is directly linked to radial growth rates, and therefore, their effects on tree vigour would be difficult to relate to survival probability estimated from retrospective growth series. This may also explain why no significant differences in survival probabilities between intermediate vigour classes have been detected.

IMPLICATIONS FOR FOREST MANAGEMENT

The results of this study highlight the strengths and weaknesses of an elaborate visual field vigour classification system. In a context where partial harvesting is used, vigour estimation is a crucial step in assigning harvest priorities for tree marking if stand improvement is sought (OMNR 2004). Tree classification systems have a long tradition, dating back to the 1840s (Rosznyay 1979). Early classifications, such as that propsed by Kraft (1884), described trees in terms of their social position, and were later amended to include qualitative measures of bole quality (Heck 1931). In 1956, Leibundgut defined the IUFRO (International Union of Forest Research Organizations) tree classification system, which combines social position, harvest priority and tree quality in a numeric code (Leibundgut 1956).

Only much later did Waring et al. (1980) define a quantitative measure of tree vigour as the ratio of basal area growth to sapwood basal area representing the amount of stemwood produced per square meter of foliage. Instead of describing trees by visually evaluating their external condition, the 'Waring vigour' index described their overall vitality. Assuming that stem growth has a low priority in carbon allocation, the amount of stemwood produced, weighted by the size of a tree's photosynthetic apparatus, was considered indicative of tree vigour (Waring et al. 1980). Other vigour measures, such as crown transparency (Millers et

al. 1991), nutrient content of needles or sapwood (Joos 1997), electric cambial resistance (Torelli et al. 1996) or chlorophyll fluorescence (Lichtenthaler and Rinderle 1988), also aimed at describing tree vigour (see Gehrig 2004 for a comprehensive review). Among these vigour-based measures, only crown transparency can be easily assessed in the field. However, crown openness can be caused by several agents and stresses (Innes 1993) that vary temporally, especially in broad-leafed trees, and therefore, it may not be adequate as a criterion for tree removal.

The vigour classification used in this study may overestimate the time-to-tree death. If moribund trees were to die within 20-25 years following vigour estimation, one would expect their survival probabilities to decline in a fashion similar to those of dead trees. However, survival probabilities of dead trees were significantly lower than those of all vigour classes in most years from 1970 onwards and in every year from 1987 to 2003 (Fig. 2.2a). This indicates that moribund trees were not declining as rapidly as dead trees were prior to their death, at least for the most recent 16 years. It is therefore doubtful that these trees would die within the predicted period.

The classification system used in Quebec, which is based on vigour-related defects in trees, has the practicality of classical tree classifications and was able to discriminate between moribund and vigorous trees, the two extreme vigour classes. It did not discriminate among the intermediate vigour classes, which suggests that the various criteria used did not affect diameter growth. However, such field vigour classifications could not adequately predict the timing of tree death with any accuracy.

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III. THE ROLE OF FOREST TENT CATERPILLAR DEFOLIATIONS AND HARVEST DISTURBANCE IN SUGAR MAPLE DECLINE AND DEATH

Henrik Hartmann & Christian Messier

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3.1 Abstract

Natural and anthropogenic disturbances may act as stresses on tree vigour according to Manion's (1981) conceptual tree disease model. According to this model, initial vigour of trees is decreased by predisposing factors that render these trees more vulnerable to severe inciting stresses, which may then cause a final vigour decline and tree death. We tested the validity of Manion's tree disease model in sugar maple (*Acer saccharum* Marsh.) by characterising the role of natural and anthropogenic disturbances in tree decline and death.

Radial growth data from ≈300 sugar maple trees that had undergone both defoliations by insects and partial harvest disturbances were used to estimate longitudinal survival probabilities as a proxy for tree vigour. Radial growth rates and survival probabilities were compared among trees of different disturbance classes, between periods of defoliation and the period of harvest disturbance, and between live and dead trees.

Manion's tree disease model correctly accounts for vigour decline and tree death in sugar maple. Tree growth and vigour were negatively affected by a first defoliation, predisposing dead trees to a second insect outbreak that initiated a final vigour decline. This was accelerated during the post-harvest period. Even the most severe anthropogenic disturbances from partial harvest did not cause, unlike insect defoliation, any growth or vigour declines in live sugar maple.

Natural disturbances acted as predisposing and inciting stresses in tree sugar maple decline and death. Anthropogenic disturbances from a partial harvest at worst accelerated a decline in trees that were already weakened by predisposing and inciting stresses (repeated insect defoliations). However, under severe climatic constraints (i.e., hot and dry summers) during the post-harvest period, anthropogenic disturbances from partial harvest may cause negative impacts on tree growth and vigour.

Keywords: Manion, Tree disease model, Disturbance, *Acer saccharum* (Marsh.), Tree mortality, Tree vigour.

3.2 Résumé

Selon le modèle conceptuel du déclin des arbres de Manion (1991), les perturbations naturelles et anthropogéniques peuvent imposer des stress et diminuer la vigueur des arbres. Ainsi, la vigueur initiale des arbres est atteinte par des facteurs prédisposants ce qui les rend plus vulnérables à des stress subséquents. Des stress incitants peuvent déclencher un déclin sévère de vigueur et la mort. Nous avons testé ce modèle avec des données d'érable à sucre (*Acer saccharum* Marsh.) en caractérisant le rôle des perturbations naturelles et anthropogéniques dans le déclin et la mort des arbres.

À l'aide de données de croissance radiale d'environ 300 érables à sucre, ayant été soumis à une coupe partielle et des défoliations répétées d'insecte, nous avons estimé des probabilités longitudinales de survie comme indicateur de vigueur physiologique. Nous avons comparé les croissances radiales et les probabilités de survie entre des classes de perturbations de coupe et entre périodes de défoliation et après coupe partielle ainsi qu'entre arbres vivants et arbres morts.

Le modèle de Manion prédit correctement la dynamique du déclin et la mort des érables à l'étude. La croissance et la vigueur ont été diminuées par une première défoliation, rendant les arbres plus vulnérables à une deuxième défoliation qui, elle, a déclenché un déclin final, accéléré durant la période après coupe. Même les perturbations anthropogéniques les plus sévères n'ont pas diminué la croissance ou la vigueur des arbres dans les arbres vivants.

Les perturbations naturelles ont joué le rôle de stress prédisposant et incitant dans le déclin et la mort d'érable à sucre. Les perturbations anthropogéniques par contre ont seulement accéléré le déclin dans les arbres déjà affaiblis et en déclin final. Toutefois, en présence de conditions climatiques très contraignantes (ex. étés chauds et secs) après coupe, les perturbations de la coupe pourraient avoir des impacts négatifs sur la croissance et la vigueur des arbres.

Mots-clés : Manion, modèle de déclin, perturbation, *Acer saccharum* (Marsh.), mortalité, vigueur.

3.3 Introduction

Tree decline is a gradual process and may require several years or even decades before tree death occurs (Pedersen, 1998b). Manion (1981) developed a conceptual tree disease model, which relates initial tree condition (i.e., tree vigour) to stress vulnerability and tree decline. According to this model long-lasting predisposing factors (e.g., soil compaction, genetic potential, air pollutants) reduce initial tree vigour and predispose affected trees, now less resistant against further disturbance, to more severe inciting stresses (e.g., defoliating insects, drought). These stresses cause sharp and irreversible vigour declines. Contributing stresses, such as secondary pathogens, may accelerate this process and act as the 'coup de grâce' for declining trees, but their role in decline may not be essential (Muller-Dumbois, 1987; Pedersen, 1998b).

However, tree vigour is an arbitrary concept describing a tree's genetic capacity to survive stress but is often used synonymously with tree vitality, the status of tree health at any one time in response to environmental stresses (Shigo, 1986). Generally, tree vigour is estimated in the field based on visual criteria, such as crown condition, stem characteristics or pathological symptoms (Ouellet and Zarnovican, 1988; Millers *et al.*, 1991; OMNR, 2004). In a more empirical approach, radial growth rates can be interpreted as an integrative measure of tree physiological condition (Gehrig, 2004), carbon balance (Givnish, 1988) and tree vigour (Dobbertin, 2005) and tree-ring chronologies can be used to estimate survival probabilities for the entire lifespan of trees (Bigler and Bugmann, 2004). Because longitudinal survival probabilities are estimated for the entire period covered by the tree-ring chronology they are a valuable tool to evaluate the impact of past stresses on tree vigour.

Stress factors in sugar maple decline, an ecologically and economically important tree species in north-eastern North America (Godman *et al.*, 1990) can result from natural disturbances, such as droughts or insect defoliations (Allen *et al.*, 1992; Parshall, 1995; Kolb and McCormick, 1993; Payette *et al.*, 1996). Sugar maple is among the principal host species of the forest tent caterpillar (FTC, *Malacosoma disstria* Hubner) whose eggs hatch in the early spring about the time of bud break and caterpillars start feeding immediately on unfolding leaves (Fitzgerald, 1995). Repeated heavy defoliations over two or more years can cause a severe reduction in radial growth, branch and twig mortality, and weaken trees by

exhausting carbon reserves for refoliation (Wargo *et al.*, 1972; Wargo, 1981). This makes trees more susceptible to other stresses, such as droughts (Renaud and Mauffette, 1991; CFS, 2001) or pathogens (Wargo and Houston, 1974).

While the impact of natural stresses on sugar maple growth and survival has been studied by several authors (e.g., Gross, 1991; Payette *et al.*, 1996; Duschesne *et al.*, 2002, 2003), studies on the impact of harvest disturbance are limited to investigations of growth release or tree physiology (e.g., Bréda *et al.*, 1995; Singer and Lorimer, 1997; Jones and Thomas, 2004, 2007) and do not consider tree survival or vigour. However, residual trees that are close to skid trails can experience disturbance in the form of root damage (Rönnberg, 2000; Ouimet *et al.*, 2005; Nadezhdina *et al.*, 2006) and soil compaction (Kozlowski, 1999) during partial harvesting. This which may lead to decreased water availability in soils (Starsev and McNabb, 2001; Komatsu *et al.*, 2007) and reduced root development (Taylor and Brar, 1991) which, in turn, may cause reductions in tree growth and survival (Murphy, 1983; Helms and Hipkin, 1986). Heavy thinning disturbs the established root-shoot equilibrium (Kneeshaw *et al.*, 2002) and the sudden opening of the canopy will cause higher photosynthetic rates (Jones and Thomas, 2007) and higher transpiration rates (Bréda *et al.*, 1995). A combination of soil compaction (reducing soil water availability) and root damage (reducing tree water uptake) with sudden canopy opening (increasing tree water use), may have an additive effect on tree water status and may cause severe post-disturbance water stress. This stress may act upon the vigour of residual trees and could be an important stress-inciting factor causing mortality.

The aim of this study was to investigate the influence of insect defoliation and harvest disturbance on radial growth and tree vigour of live sugar maple (*Acer saccharum* Marsh.). We addressed the following questions in our study. (1) Is observed tree decline driven, as predicted by Manion's (1981) conceptual model, by an interaction of predisposing, inciting and contributing stresses, and can these stresses be associated with growth declines and decreases in survival probability? (2) How is growth and vigour of residual trees affected by disturbances from partial harvests? (3) Have FTC defoliations and harvest disturbances a similar impact on tree radial growth and vigour? (4) Can these anthropogenic and natural factors act as predisposing, inciting or contributing stresses in vigour decline and tree death?

3.4 Materials & methods

STUDY REGION

Sugar maple trees were studied in forest stands near Temiscaming in western Quebec, Canada (46°43' north, 79°04' west). The forests of this region are part of the western sugar maple-yellow birch bioclimatic domain (Robitaille and Saucier, 1998). Mean annual temperatures range from 2.5-5.0°C, the growing season spans 170-180 days, and mean annual precipitation is 800-1000 mm, with snowfall comprising roughly 25% of total precipitation (Gosselin *et al.*, 2000). Soils of the region originate mainly from glacial tills (Robitaille and Saucier, 1998).

STUDY PLOTS

In 2004 and 2005, 19 plots (26 x 56 m) were established in stands that had undergone a selection cut in either 1993 or 1994. The selection cut aimed at removing individual trees of low growth potential by reducing average pre-harvest stand density of 27 m^2/ha to an average 21 m^2/ha. Sugar maple was the most abundant species (~ 68% of total post-harvest basal area), follwed by yellow birch (*Betula alleghaniensis* Britton, ~ 18%), and red oak (*Quercus rubra* L., ~ 3.5%), and some other species (e.g., *Fagus grandifolia* Ehrh., *Thuja occidentalis* L., *Tsuga canadensis* [L.] Carr., *Abies balsamea* [L.] P. Mill., *Picea glauca* [Moench] Voss, and *Acer rubrum* L.) occurred in smaller proportions.

In these plots we measured the diameter and mapped the position of all live and dead trees >9.1 cm in diameter at breast height (*dbh*, 1.3 m above ground), together with all stumps (diameter at stump height, dsh, ≈ 0.5 m above ground), from the 1993/1994 harvest. Mapping was achieved by laying out a virtual grid on the forest floor. The plot center line provided the y-coordinates and perpendicular distances from this line to the trees (x-coordinates) were measured using a Hägloff Vertex III® hypsometer (Haglöf Sweden AB).

We also mapped skidding trail networks from the 1993/1994 harvest using soil disturbance, tree positions and regeneration as indicators for the original path. Path width was assumed to be 4 m, a conservative estimate of the original skid trail width.

TREE GROWTH DATA

Growth data for live trees were obtained from increment cores (three per tree at 1.3 m above ground) taken from trees within the 19 plots. However, due to their rarity, recently dead trees (1993 or later) had to be searched for throughout the entire area harvested in 1993 and 1994. We used presence of bark and fine branches and absence of advanced trunk decay as selection criteria for recently dead trees (Sénécal et al. 2003).

To preclude growth-independent factors from influencing the parameter estimates of the growth-driven survival probability model (see below), cross sections of tree trunks at 1.3 m above ground level were collected only from dead trees without any evidence of obvious causes of instantaneous death (uprooting, bole breakage, etc.).

A total of 323 live and 56 dead trees were growth-sampled, and were distributed roughly uniformly among three *dbh* classes (19.1-29.0 cm, 29.1-39.0 cm, 39.1-49.0 cm). These diameter limits ($\geq$19.0 cm and $\leq$49.0 cm) were imposed to prevent heavily suppressed (i.e., smaller diameter) and senescent (i.e. larger diameter) trees from being sampled. Because both suppression and senescence can have a strong influence on growth rates, impacts of defoliation and harvest disturbance on growth may have obscured in very small and very large trees.

Increment cores and cross-sections were progressively sanded to make the final cell layer in each tree-ring clearly visible. Tree-rings were then measured using a microscope equipped with a computer-assisted micrometer (0.001 mm precision). In most cases, at least two cores per tree were readable. For the dead trees, two radii per tree were chosen from cross sections for radial growth measurements. We averaged these tree-level measurements to account for intra-tree variability of radial increment due to growing conditions or leaning (Kienholz, 1930; Peterson and Peterson, 1995). This yielded a single growth chronology per tree.

We took a subsample of dominant live trees to construct a master chronology by progressively adding highly correlated tree-ring series (using the program COFECHA, Holmes, 1983) to the already existing ones. We considered r-values $\geq$0.3 as good cross-correlations with the master chronology (Tardif et al., 2001), which had a final overall cross-correlation coefficient of 0.479 among the 29 individual tree chronologies.

We cross-dated (matching of tree-rings with calendar years) live and dead tree-ring series based on (1) visual examination of marker years (mainly a severe growth decline in 1971 and 1988) and (2) using cross-correlation coefficients of chronology segments with the master chronology. COFECHA assisted in detecting missing or false rings in individual segments of tree-ring series. In suspect cases, we identified false or missing rings on the cores or cross-sections, and added or removed these from the series. Corrected series were then run again in COFECHA to verify the cross-correlation with the master chronology. We also collected data from 90 live yellow birch trees from within the plots and constructed a yellow birch chronology by the same means as described above. The resulting chronology contained data from 20 individual trees and had a cross-correlation coefficient of 0.392.

Tree-ring series were standardised by dividing each individual tree-ring series by its growth trend estimate, using a cubic smoothing spline. This procedure was done after visually checking the adequacy of the growth trend estimate (close match of growth trend estimate with growth chronology) and produced dimensionless ring-width indices that can be more adequately compared among trees at different ages and from different sites. Standardising was done using the `i.detrend` function from the contributed `R` package `dplR` (Bunn, 2007) in the `R` software environment for statistical computing and graphics (version 2.6.0; R Development Core Team, 2007).

NATURAL DISTURBANCES

We identified periods of FTC outbreaks by subtracting a non-host (yellow birch) chronology of growth indices from chronologies of growth indices of the host species, sugar maples (Swetnam *et al.*, 1985). Residuals from the mean of the yellow birch (By) series are first rescaled to the variance of the host series that yielded predicted residual indices (PRI), which were then subtracted from the raw sugar maple (Ms) indices to produce the corrected sugar maple indices (*CI*, Swetnam and Lynch ,1989):

$$PRI = \frac{SD_{Ms}}{SD_{By}} * \left(Index_{By} - Mean_{By}\right) \quad (1)$$

$$CI = Index_{Ms} - PRI \quad (2)$$

We considered periods as inferred insect outbreaks when corrected indices were negative for at least 3 consecutive years because FTC outbreaks are known to last about 2 to 4 years (Fitzgerald, 1995). Also, at least one of these indices was to be at least one standard deviation below the mean of the series. This allowed a close match of the inferred outbreak frequency with the observed approximate average frequency of FTC outbreaks in this region (9+ years, MRNFPQ, 2002).

MEASURES OF ANTHROPOGENIC DISTURBANCE

Disturbance from logging (i.e., machinery traffic causing soil compaction and root damage or major canopy removal) did not occur until the 1993/1994 selection cut in the stands under investigation (D Boileau, MRNFQ, Canada, 'pers. comm.').

Sudden exposure to higher light levels due to partial cutting

Because harvesting was done 11 years prior to our field work, we could not measure changes in light levels directly and therefore used simulation. To achieve this, *dsh* measurements of tree stumps were converted to *dbh* using existing conversion tables (MRNFPQ, 2003). These *dbh* estimates were then used to virtually resurrect harvested trees (see below). The resulting pre-harvest *dbh* maps were then entered into the simulation model SORTIE to estimate light availability for individual trees (Pacala et al., 1993, 1996).

SORTIE was parameterised with regional parameters of tree species allometry and species-specific light extinction coefficients (Canham et al., 1994; Poulin and Messier, 2007; Lefrançois et al., 2008; M Beaudet, UQAM, Montreal, Canada, 'unpubl. res.'). Based on these parameters, SORTIE modelled tree and crown dimensions of each tree and then computed light availability for each tree as the seasonally averaged percentage of full sun (Canham, 1988). This routine was run initially on the plots, with the inclusion harvested and recently dead trees, and then with residual trees only, viz., the actual post-harvest plots. We estimated light availability individually for each tree in the centres of the simulated crowns at 0.75*crown height. The ratio of post- over pre-harvest light availability was then computed as our measure of changes in light conditions.

Soil disturbance in the proximity of trees

Based on the assumption that tree crown dimensions can be predicted from tree diameter, and that tree crown dimensions are a proxy for tree root system coverage (Tubbs, 1977), a circular 'influence zone' around each tree was estimated based on species-specific parameters of diameter-crown relationships, which yielded diameter-dependent influence zones with radii (m) = 0.100**dbh* (cm) for sugar maple (Beaudet *et al.*, 2002). The intersection of these influence zones with the mapped skidding trails yielded a proportion of the influence zone that had been disturbed by machinery traffic. This proportion, expressed as a percentage of the total area of the influence zone, was our measure of soil disturbance close to trees.

LONGITUDINAL SURVIVAL PROBABILITY ESTIMATION

Longitudinal survival probabilities served as a proxy for tree vigour in this study. Of the 321 live trees, 56 individuals (i.e., a number equivalent to the sample size of dead trees) were randomly selected and used to parameterise the survival probability model. Estimations were based on a longitudinal logistic regression approach (Bigler and Bugmann, 2004), which uses growth data from the entire lifespan of the trees. Predictor variables (e.g., mean values and linear regression coefficients) were computed within a moving window of *n* years across the time-series. Data points containing the last year of growth of a dead individual are marked as 'dead' data points. All other data points are marked as 'live' data points.

In a companion study (Hartmann, *et al.*, in press) we selected the best model supported by the data from a set of candidate models (with different predictor variables) based on Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). The resulting survival probability model was:

$$P(survival) = \frac{e^{-7.115+2.017 av3\log+0.006 slp5}}{1+e^{-7.115+2.017 av3\log+0.006 slp5}} \qquad (3)$$

where *P(survival)* is the probability that an individual survives, *av3log* is the log-transformed average over the previous 3 years of radial growth and *slp5* is the linear trend over the previous 5 years of radial growth.

Parameter estimation was undertaken within R (version 2.6.0; R Development Core Team, 2007), using maximum likelihood. Non-parametric confidence intervals for the parameter estimates were computed with the `bootcov` bootstrap resampling procedure from the `Design` library (Harrell, 2005), based on 1000 repetitions, with the 25th and the 975th quantiles serving as interval limits. To correct for underestimation of the true variance and confidence interval width due to the interannual correlation of longitudinal tree-ring data, the `bootcov` function substitutes cluster (= within tree) sampling with replacement for the usual simple (= among trees) sampling with replacement. This modification resulted in parameter estimates that can be regarded as unbiased.

Model performance was estimated with Somer's D_{XY} index (Somers, 1962), which is indicative of the model's discriminative ability and is closely related to the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Engelmann *et al.*, 2003). The `Design` bootstrap resampling procedure `validate.lrm` (Harrell, 2005) was used to account for over-optimistic classification measures when validating models on training data (data specificity). The `validate.lrm` procedure eliminates overfitting-induced optimism of D_{XY} and produces a more conservative estimate of the model's discriminative ability (Harrell, 2001). The model used in this study had a D_{XY} value of 0.783, which corresponded to an AUC of 0.892 and indicated excellent model performance (Manel *et al.*, 1999, Table 3.1).

Table 3.1
Parameter estimates, bootstrapped 95% confidence intervals (CI), AUC (ROC) and optimism-corrected D_{XY} of the logistic survival probability model

		CI (95%)			
Variables	Estimate	Lower	Upper	D_{XY}	AUC
Intercept	-7.115	-8.974	-5.337	0.783	0.892
av3-log	2.017	1.713	2.375		
slp5	0.006	0.004	0.007		

Interpretation of survival probabilities

The above described procedure led to a very unbalanced data distribution (i.e., many live data points and few dead data points) and yields, using logistic regression, survival probability estimates biased towards the more abundant group (Fielding and Bell, 1997). Hence, survival probability estimates were all very close to one and could not be interpreted directly, i.e. as absolute measure of probability of survival, unless adjustments for the unbalanced data distribution were undertaken. However, in our study, survival probabilities were interpreted only as a relative measure of tree vigour among disturbance classes of trees (see below), so threshold adjustments were unnecessary.

COMPARISON OF GROWTH INDICES AND SURVIVAL PROBABILITIES AMONG DISTURBANCE CLASSES AND DEAD TREES

Live trees with available growth data were grouped into 4 anthropogenic disturbance classes: (1) trees with neither machinery disturbance in their proximity nor a substantial (>50%) increase in post-harvest light levels (N = no disturbance, n=134), (2) trees with machinery disturbance in their proximity, but no substantial increases in light levels (M = machinery, n=71); (3) trees with a substantial (>50%) increases in post-harvest light levels, but no machinery disturbance (L = light, n=28); and (4) trees with both substantial (>50%) increases in post-harvest light levels and with machinery disturbance (L&M = light and machinery, n=16).

Of the 321 live trees, 249 fell within these classes, while the remainder contained trees with either no machinery disturbance but light increases ≤50% (n=51), or trees with machinery disturbance but with light increases ≤50% (n=21). Because dead trees (D, n=56) had to be searched for outside our sampling plots, we could compute disturbance levels for these trees.

Since ring-width measurement and survival probabilities are usually not normally distributed, we used the non-parametric Kruskal-Wallis test for annual comparisons of ring-width indices among disturbance classes and with dead trees in the years prior to and following harvest (1990-2004). We employed a non-parametric simultaneous rank test

procedure for multi-comparisons using the npmc function from the R package npmc (Helms and Munzel, 2008). This procedure is based on estimations of simultaneous relative effects and variance among pairs, does not assume continuity of the underlying distribution functions (as Wilcoxon or other ranking procedures do) thereby allowing arbitrary ties. The procedure can be applied to all relevant multiple testing problems in the one-way layout and derives the test statistic (W_N^{BF}) and *P*-values with the Behrens-Fisher test (Munzel and Hothorn, 2001). Survival probabilities were analysed with the same procedure described above.

To test for differences between FTC defoliation and harvest disturbances, we used corrected growth indices because these are assumed to be free of the effects of climate and other environmental factors on growth rates (Swetnam *et al.*, 1985). We selected the 1986-1992 FTC outbreak, which had the strongest influence on growth rates among all inferred and documented FTC outbreaks. We compared the averaged (within individual trees) growth indices over this period with those over the 1994-1998 post-harvest period (and just before the onset of the next FTC outbreak in 1999), within each disturbance class and within dead trees. Since we compared observations within growth chronologies of the same trees, we used a Wilcoxon signed-rank test. This test requires equal sample sizes between the two groups, a condition that was not met for dead trees for the 1994-1998 period due to mortality dropout. We therefore compared data from this period with a random subsample (without replacement) of the 1986-1992 period, applied a Wilcoxon signed-rank test on this balanced sample, repeated this procedure 1000 times and averaged test *P*-values.

DEFINITION OF STRESSES ON TREE GROWTH AND VIGOUR

According to Manion's (1981) conceptual tree disease model, predisposing factors, such as genetic potential or soil compaction, can determine initial tree vigour and, therefore, a tree's vulnerability to further stresses. These factors are difficult or even impossible to assess since an unambiguous benchmark for the absence of stress would have to be defined. However, predisposing factors have a diffuse impact on tree vigour, allowing trees to survive but with modified vital functions (Waring, 1987). In this study, predisposing factors are defined as stresses with a moderate impact on tree vitality, i.e., on tree vital functions as

measured by radial growth. These stresses decrease radial growth levels but do not lead ultimately and directly (without further stress) to tree death.

In contrast, according to Manion (1981), inciting factors are severe stresses, such as defoliations or drought, which cause severe vigour declines and ultimately lead to tree death. We used this definition with respect to radial growth and survival probabilities. In an accompanying study (H. Hartmann, unpublished data), trees with survival probabilities permanently below 0.987 eventually died (data not shown). Hence, this value can be considered a threshold for definite vigour decline and a benchmark for inciting stresses.

Contributing stresses may not play an essential role in tree decline (Muller-Dumbois, 1987, Pedersen, 1998b) but can act as the 'coup de grâce' for declining trees by accelerating their decline. We defined contributing stresses as decreases in survival probabilities when these had already fallen below the threshold of definite vigour decline.

SUMMER CLIMATE DATA AS INDICATOR OF GROWTH CONDITIONS

We computed mean summer monthly precipitation and temperature (April-August) as an indicator of climatic growth conditions from monthly climate data of the two closest nearby (~ 60 km) weather stations (Environment Canada, http://climate.weatheroffice.ec.gc.ca).

3.5 Results

GROWTH DYNAMICS OF UNDISTURBED TREES

A comparison of average growth rates from 1910 to 2004 for undisturbed (by harvest) live versus dead sugar maple trees showed that they both experienced a sudden increase in growth rates in the late 1950's (Fig. 3.1a). Shortly after this increase, growth rates of dead trees started to deviate from those of live trees (about 1960). In 1971, a major drop in growth rates of both live and dead trees occurred, which was followed by a continuous decline in both groups. This decline was followed, in 1988, by another major drop in growth rates of both live and dead trees (Fig. 3.1a). The 1993/1994 harvest (indicated by the arrow in Fig. 3.1a) caused a temporal increase in growth rates of dead trees, which then declined and died. In live trees, the growth decline in 1988 was followed by an increase in growth to levels prior to 1988, which were then maintained until 2004 (Fig. 3.1a).

Average ring-width indices do not show the difference between live and dead tree growth patterns as clearly, at least for earlier years. Until 1965, standardised growth rates of dead trees were more variable and oscillated around live tree growth indices (Fig. 3.1b). From 1965 to 1995, growth indices of live and dead trees were almost identical and both groups experienced a major drop in 1988, followed by an increase. From 1995 onwards, shortly after the 1993/1994 harvest (indicated by the arrow in Fig. 3.1b), growth indices of dead trees declined whereas those of live trees maintained increases in growth levels until 2004 (Fig. 3.1b).

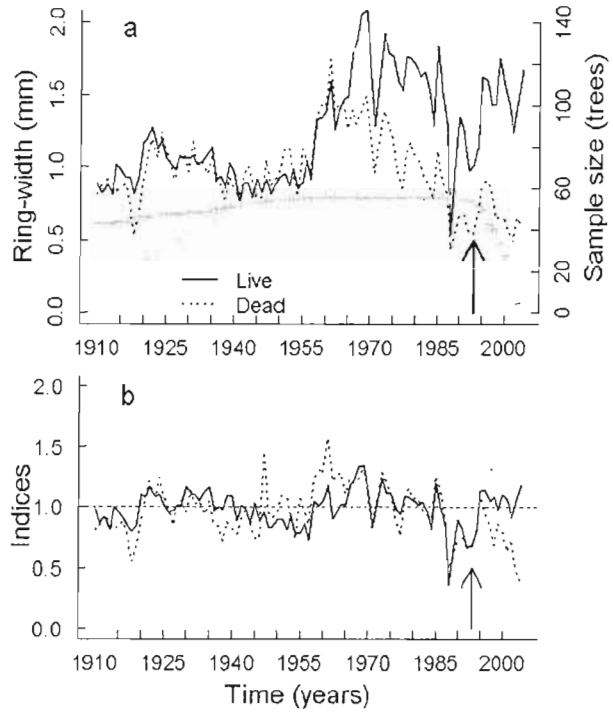

Figure 3.1 (a) Average ring-width (mm, lines) and sample size (trees, symbols) chronologies (1910-2003) of undisturbed (by harvest) live (solid line) and dead (dotted line) trees. (b) Average growth index chronologies (1910 – 2003) of undisturbed (by harvest) live (solid line) and dead (dotted line) sugar maple trees. Arrows indicate the year of the selection harvest.

Rescaled indices of yellow birch showed a growth pattern different from that of sugar maple during several periods, especially in the 1930's, 1940's and 1960's (Fig. 3.2a). Corrected sugar maple ring-width indices showed that growth of dead trees was affected more than that of live trees by FTC defoliations from the 1930's until the mid-1940's, but dead trees exhibited higher growth rates from about 1945 until 1965 (Fig. 3.2b). Decreases in growth rates of dead trees lasted longer than those of live trees during the 1986-1992 outbreaks (see area under the curve in Fig. 3.2b). Although dead trees achieved a brief and small increase in growth rates in 1994 and 1995, growth declined again shortly after harvest in 1996 (indicated by the thin arrow in Fig. 3.2b) and trees died shortly afterwards.

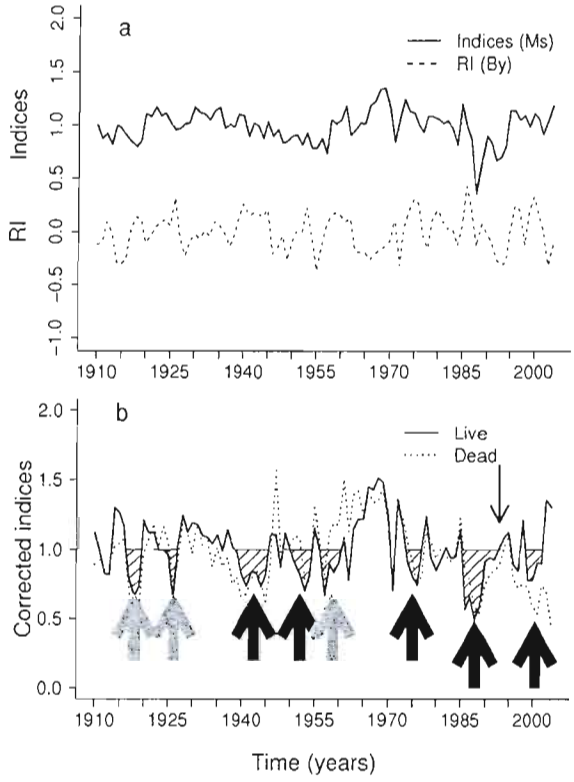

Figure 3.2 (a) Averaged ring-width indices (1910 – 2003) of undisturbed (by harvest) sugar maple trees (n=134, same as in Fig. 3.1b) and rescaled indices (RI) of yellow birch trees (n=20), a non-host species of the forest tent caterpillar. (b) Corrected ring-width indices of sugar maple trees obtained by subtracting RI in (a) from the host species (sugar maple) indices in (a). Cress hatched areas in (b) are periods of inferred (grey block arrows) or documented (black block arrows) FTC defoliations (see text for details). The down facing arrow in (b) indicates the year of the selection harvest.

We identified eight insect outbreaks during the period from 1910 to 2004 which translated into an average outbreak cycle length of 11.75 years and an average outbreak length of 4.6 years (data not shown). All but the 1957-1960 FTC outbreak could be confirmed by MRNFQ survey data available for 1938-2002. However, the ministry survey indicated a continuous occurrence of FTC defoliations from 1950 until 1956, suggesting that both the 1950-1954 and 1957-1960 growth declines were caused by this single FTC outbreak.

GROWTH DYNAMICS OF DISTURBED TREES

To evaluate the impact of harvest disturbance on radial growth, we examined growth indices for the 1990 – 2004 period, i.e., three years prior to until 10 years after partial harvest. In 1990, growth indices of dead trees were significantly different from those of undisturbed live trees only (Table 3.2). From 1991 until 1994, there were no significant differences in growth indices among disturbance classes. Indices of dead trees were significantly different from all live trees in 1998, 2001, and 2003, from L, M, and N trees in 1999 and 2000, from L and L&M trees in 1995, 1996, and 1997, and from N trees in 1995 (Table 3.2). Among live trees only, the growth indices of L trees were different from those of M trees in 1995, 1997, and 1997 and from N trees in 1995 (Table 3.2).

The 1986-92 FTC defoliation had a greater impact on corrected growth indices of live sugar maple than any of the harvest disturbance types, but this was not the case for dead sugar maple. Means of the averaged corrected indices during defoliation varied between 0.627 for L trees and 0.727 for N trees (Table 3.3). During the post-harvest period (1994-1998), corrected indices were consistently higher for all trees, ranging from 0.809 (D) to 1.267 (L) (Table 3.3). Differences in average corrected indices between periods of natural and anthropogenic disturbance were highly significant (P <0.001) within disturbance classes of all live trees, but not significant for dead trees (Table 3.3).

Table 3.2
Behrens-Fisher tests on relative effect estimates of ring-width indices (1990 – 2003) between disturbance classes using a non parametric simultaneous rank test procedure. Only significant ($P<0.05$) tests are shown

			Relative effect estimate						
Year	Comparison	n	Effect	CI (lower)	CI (upper)	Var.	SE	W_N^{BF}	P
1990	D vs. N	189	0.648	0.518	0.778	0.382	0.045	3.290	0.021
1995	D vs. L	78	0.759	0.592	0.927	0.251	0.057	4.571	0.002
	D vs. L&M	66	0.719	0.531	0.906	0.267	0.064	3.441	0.019
	D vs. N	184	0.669	0.506	0.832	0.563	0.055	3.057	0.040
	L vs. M	99	0.296	0.106	0.487	0.413	0.065	-3.155	0.035
	L vs. N	162	0.281	0.091	0.471	0.671	0.064	-3.403	0.020
1996	D vs. L	71	0.694	0.512	0.877	0.273	0.062	3.133	0.034
	D vs. L&M	59	0.725	0.524	0.926	0.275	0.068	3.301	0.024
1997	D vs L	69	0.748	0.575	0.921	0.242	0.059	4.189	0.003
	D vs. L&M	57	0.729	0.537	0.920	0.245	0.066	3.485	0.015
	L vs. M	99	0.302	0.112	0.492	0.420	0.065	-3.035	0.039
1998	D vs. L	67	0.799	0.638	0.960	0.202	0.055	5.455	0.000
	D vs. L&M	55	0.747	0.551	0.942	0.244	0.067	3.705	0.010
	D vs. M	110	0.681	0.502	0.861	0.412	0.061	2.965	0.047
	D vs. N	172	0.729	0.566	0.893	0.534	0.056	4.115	0.004
	L vs. M	99	0.259	0.082	0.435	0.359	0.060	-4.012	0.005
1999	D vs. L	62	0.777	0.593	0.962	0.242	0.062	4.441	0.002
	D vs. M	105	0.692	0.502	0.883	0.437	0.065	2.979	0.047
	D vs. N	165	0.715	0.534	0.895	0.615	0.061	3.519	0.016
2000	D vs. L	55	0.749	0.545	0.953	0.261	0.069	3.611	0.014
	D vs. M	99	0.737	0.543	0.932	0.428	0.066	3.610	0.013
	D vs. N	159	0.728	0.540	0.917	0.646	0.064	3.584	0.014
2001	D vs. L	45	0.749	0.520	0.978	0.267	0.077	3.234	0.030
	D vs. L&M	34	0.754	0.503	1.005	0.243	0.085	3.009	0.046
	D vs. M	89	0.767	0.557	0.977	0.445	0.071	3.775	0.010
	D vs. N	141	0.758	0.550	0.965	0.688	0.070	3.688	0.012
2003	D vs. L	30	0.872	0.572	1.172	0.168	0.075	4.973	0.022
	D vs. L&M	20	0.880	0.556	1.204	0.130	0.081	4.708	0.027
	D vs. M	72	0.845	0.558	1.132	0.368	0.072	4.822	0.024
	D vs. N	113	0.870	0.629	1.111	0.407	0.060	6.174	0.009

Table 3.3
Mean, standard error (SE) and range of averaged corrected indices during FTC outbreak (1986 – 1992) and harvest disturbances (1994 – 1998). *P* values refer to a Wilcoxon signed-rank test between periods. Negative values are in parentheses

Disturbance class	Natural disturbance			Harvest disturbance			
	Mean	SE	Range	Mean	SE	Range	*P*
N	0.727	0.185	0.260 – 1.281	1.033	0.255	0.561 – 2.048	<0.001
M	0.704	0.177	0.329 – 1.230	0.972	0.248	0.260 – 1.664	<0.001
L	0.627	0.234	0.223 – 1.022	1.267	0.372	0.495 – 2.047	<0.001
L & M	0.687	0.151	0.283 – 0.876	1.156	0.292	0.614 – 1.752	<0.001
D	0.688	0.247	(0.189) – 1.252	0.809	0.419	0.132 – 1.859	0.352

Dead trees exhibited the first signs of vigour decline in 1977 (Fig. 3.3) following the FTC outbreak in 1974-1976. Vigour of dead trees was lower before the 1986-1992 FTC outbreak than vigour of live trees and was followed by a greater vigour decline during the 1986-1992 FTC outbreak than in live trees. Dead trees never regained their pre-FTC outbreak vigour levels and their vigour stayed below levels of live trees (Fig. 3.3). Multiple comparisons (Behrens-Fisher tests) indicated that survival probabilities of dead trees were significantly different from those of all four disturbance classes from 1992 until 2002 (Fig. 3.3, Table inset). In the post-harvest period (1994 onwards), no differences of survival probabilities among disturbance classes were detected (Fig. 3.3).

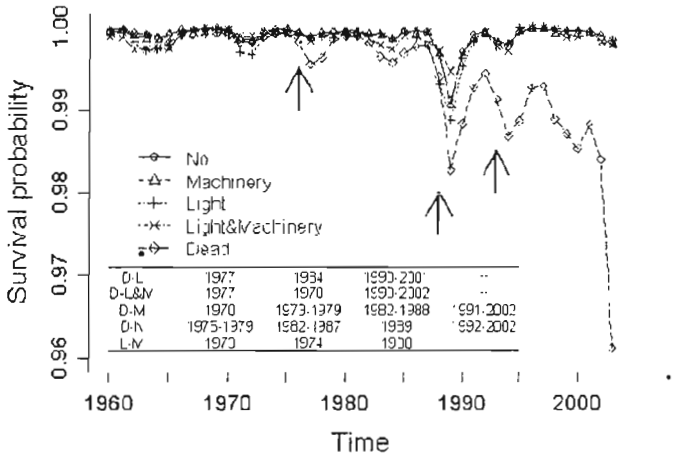

Figure 3.3 Average survival probabilities of live and dead sugar maple trees from 1960 – 2003. Table inset specifies years of significant differences (P <0.05) between pairs of disturbance classes and dead trees and among disturbance classes. Arrows indicate the most severe years of FTC outbreaks (1974-1976, 1986-1992) and the partial harvest (1993). The horizontal line indicates a critical probability threshold (P[Y=1] =0.987) for a definite vigour decline (see text for details).

Mean summer temperatures were only slightly above the long-term average (1910-2003) in the years following harvest (1994-1997) and mean summer precipitation was above average in 1994, on average in 1995 and again above average in 1996 (Fig. 3.4).

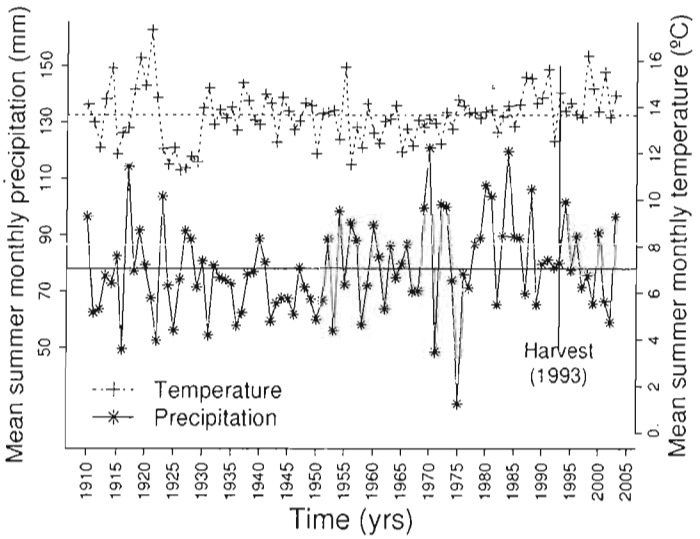

Figure 3.4 Mean summer (April-August) monthly precipitation (solid line with stars) and temperature (dotted line with crosses) computed from climate data covering the years 1910-2003. Horizontal lines indicate the long-term mean precipitation and temperature across these years. The vertical line indicates the year of the partial harvest (1993).

3.6 Discussion

THE NATURE OF PREDISPOSING AND INCITING STRESSES AND THEIR INTERACTION

In our study, dead trees were predisposed to inciting stresses by a first FTC defoliation in 1974-76 which decreased their initial vigour. The 1986-1992 FTC defoliation acted then as an inciting stress having a longer lasting and more severe negative effect on growth rates and vigour of dead trees than the 1974-76 outbreak. Although growth rates and survival probabilities of dead trees temporarily recovered shortly after harvest, their decline resumed and accelerated drastically from 1997 onwards (Fig. 3.3). Harvest disturbances may have contributed to this acceleration as a contributing stress in these already weakened trees.

Successive defoliation events that can readily weaken more sensitive trees and trigger sugar maple decline (Kolb and McCormick, 1993; Payette *et al.*, 1996). Carbon reserves of dead trees may have been already reduced from repeated previous defoliations (Parker and Houston, 1971) and the 1986-1992 severe defoliation may then have acted as inciting stress in the decline of already weakened trees (Horsley *et al.*, 2002). In live trees, more abundant carbon reserves may explain their greater potential for recovery, which allowed to quickly rebuild leaf area and subsequently, their photosynthetic apparatus (Landhäusser and Lieffers, 2002).

Sugar maple tree decline and death was driven by an interaction between predisposing and inciting stresses, as suggested by Manion's (1981) conceptual tree disease model. Similarly, Hogg *et al.* (2002) found that FTC defoliations combined with other environmental stresses led to reduced growth and crown dieback in trembling aspen (*Populus tremuloides* Michx.). Our results are in general agreement with those of other researchers who identified defoliating insects (Payette *et al.* 1996), fungal pathogens (Cherubini *et al.*, 2002; Marçais and Bréda, 2006) or drought (Pedersen, 1998a; Suarez *et al.*, 2004) as inciting stresses in tree decline and death.

IMPACT OF ANTHROPOGENIC DISTURBANCES FROM PARTIAL HARVEST ON TREE GROWTH AND VIGOUR

Radial growth rates of live trees in all harvest disturbance classes quickly regained or even surpassed pre-disturbance growth levels after harvest disturbances and did not show a growth stagnation known as 'thinning shock' (e.g., Staebler, 1956; Harrington and Reukema, 1983). On the contrary, trees with strong increases in light levels showed the greatest post-disturbance growth increases lasting until 1998 (Table 3.2). Although photoinhibitive effects of significant and sudden increases in light levels have been observed in seedlings of shade-tolerant beech (Fagus sylvatica L.; Tognetti et al., 1997) and in saplings of shade-tolerant sugar maple (Naidu and DeLucia, 1997), this does not seem to be the case for adult sugar maple trees in our study, even though mean increases in light levels were remarkably high (> 600%, data not shown). Instead, acclimatisation of shade leaves in the lower canopy to higher light availability close to canopy gaps seemed to have increased photosynthetic rates (Jones and Thomas 2007) and this translated into higher growth rates (Jones and Thomas 2004). Hence, sudden changes in light availability from partial harvest did not have the potential to act as a stress causing growth declines but rather improved tree vitality.

Soil disturbance is thought to negatively impact radial growth of trees (Clayton et al., 1987) through its effects on soil physical properties (Kozlowski, 1999) or potential damage to the root system (Waesterlund, 1992) but also through potentially resulting fungal infections of the tree root system (Nadezhdina et al., 2006). However, growth indices of trees that experienced machinery disturbance were only lower than those of trees with increased light levels, but not significantly different from those of undisturbed trees (Table 3.2). This is surprising since these trees had a mean soil disturbance of 34.7 % (Table 3.1). The soil texture in the study plots (which was either sandy, sandy loam or, in one plot, rocky) may explain the absence of negative effects of machinery disturbance on growth. Coarse-textured soils are not easily compacted (Horn, 1988; McBride and Joosse, 1996) and the dense root network in the humus layer, formed by the abundant woody understory vegetation in the studied maple stands (mostly tree regeneration, beaked hazel [*Corylus cornuta* Marsh.], and hobblebush [*Viburnum lantanoides* Michx.]), may increase soil strength and thus resistance to mechanical forces from logging equipment (Waesterlund, 1989). Machinery disturbance

apparently did also not cause fungal infections of the tree root systems and associated severe growth declines as has been observed, for example, in trees infected with root rot (Mallet and Volney, 1999; Cherubini et al., 2002).

COMPARING IMPACTS OF INSECT OUTBREAKS AND HARVEST DISTURBANCES ON RADIAL GROWTH AND TREE VIGOUR

Average corrected growth indices were lower during natural disturbance than during the post-harvest period (Table 3.3), indicating that FTC defoliation had a stronger negative effect on growth rates than any harvest disturbance. These results show that disturbances from partial harvest, even in their most severe form, have no significant negative effect on tree growth. It may be noted, however, that we did not sample trees that had incurred obvious damage from harvest (uprooting, bole breakage, girdling, etc.). This type of 'disturbance' would most probably cause growth reduction and has been found to cause high post-harvest tree mortality (Nyland, 1994).

3.7 Conclusions

Our findings showed that disturbances from partial harvest, at worst, can act as contributing stresses in trees that are already greatly weakened by predisposing and inciting stresses, in our study FTC defoliations. Since the whole range of disturbance severity caused by a partial harvest was sampled in this study, we must conclude that harvest disturbances did not contribute to maple decline and death. However, favourable climatic conditions did not impose severe constraints on tree growth in the post-harvest period. Hence, the impact of harvest disturbance may have been different if climatic conditions, especially precipitation, had been less favourable for growth (Hanson *et al.*, 2001). The sudden exposure to sunlight from thinning may then impose an additive constraint on tree water status (Warren *et al.*, 2001) and this may impose a stress that not only decreases radial growth rates but may act as inciting stresses in tree decline and death (Pedersen, 1998b).

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IV. EFFECTS OF ABOVE AND BELOW GROUND PARTIAL HARVEST DISTURBANCE ON RESIDUAL SUGAR MAPLE (*Acer saccharum* Marsh.) GROWTH AND WATER STRESS

Henrik Hartmann, Christian Wirth, Christian Messier & Frank Berninger

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4.1 Abstract

Partial harvesting is known to modify both above and below-ground resource availability but may also induce some direct and indirect stress to residual trees due to machinery traffic and sudden changes in light levels. We studied sugar maple (*Acer saccharum* Marsh.) trees in stands that had undergone a selection harvest 11 years prior to sampling to verify whether sudden increases in light availability and soil disturbance from machinery would influence growth rates and could lead to water stress.

We selected trees that had experienced either no disturbance from partial harvest, soil disturbance only, sudden increases in light availability only or both disturbances. We analyzed stem radial growth rates and stable carbon isotope composition ($\delta^{13}C$) of stem wood with an annual resolution from 10 years prior to until 10 years after partial harvest.

Our results showed that disturbances from partial harvest did not have a negative influence on growth rates or on maple water status. Although trees that experienced increases in light availability had higher $\delta^{13}C$ after harvest (indicating water use efficiency) increased growth rates suggest that these trees did not experience any water stress. Also, trees with soil disturbance did not show any signs of water stress. These results may partly be due to favorable climatic conditions (abundant precipitation and mild temperature) in the years following harvest and could be different under more severe climatic conditions.

Keywords: Selection cut, light availability, soil disturbance, tree water status.

4.2 Résumé

La coupe partielle redistribue des ressources du milieu (lumière, eau, nutriments) et améliore ainsi les conditions de croissance pour un nombre restreint d'arbres résiduels. Une plus grande interception de lumière augmente le taux de photosynthèse et la croissance à l'échelle de l'arbre mais également la conductivité stomatale et la demande en eau. Cette demande est habituellement contrebalancée par une plus grande disponibilité en eau par l'éclaircie du peuplement, mais la circulation de la machinerie près des arbres peut causer une compaction du sol et des dommages aux racines et ces perturbations peuvent ainsi réduire la disponibilité en eau au sol et / ou l'absorption d'eau par les arbres affectés.

Nous avons étudié l'érable à sucre (*Acer saccharum* Marsh.) dans des peuplements ayant subi une coupe partielle 11 ans avant l'échantillonnage afin de vérifier si l'augmentation soudaine de la lumière jumelée à des perturbations du sol par la machinerie influence la croissance radiale et cause un stress hydrique.

Nous avons sélectionné des arbres échantillons selon quatre classes de perturbation : (1) aucune perturbation, (2) perturbation de la machinerie à proximité seulement, (3) augmentation de la lumière seulement et (4) les deux perturbations simultanément. Nous avons analysé la croissance radiale et le ratio isotopique ($\delta^{13}C$) des cernes de croissance à résolution annuelle de 10 ans avant jusqu'à 10 ans après coupe partielle.

Nos résultats montrent que les perturbations de la coupe n'ont pas eu d'impact négatif sur la croissance ni l'état hydrique des arbres. Quoique les arbres ayant vécu une augmentation de la lumière démontraient une augmentation de $\delta^{13}C$ après la coupe (probablement due à une augmentation du taux photosynthétique), cette augmentation a été accompagnée par une hausse de la croissance radiale indiquant l'absence d'un stress hydrique. Similairement, les ratios isotopiques des arbres avec perturbation du sol n'ont pas indiqué aucun signe de stress hydrique. Toutefois, ces résultats pourraient être dus, au moins en partie, à des conditions météorologiques estivales favorables (précipitation abondante, température modérée) dans les années suivant la coupe. Sous conditions plus contraignantes dans les années suivant la coupe (étés secs et chauds) les résultats de cette étude pourraient être différents.

Mots-clés : Coupe de jardinage, disponibilité de lumière, perturbation du sol, état hydrique des arbres

4.3 Introduction

Partial harvests remove varying proportions of canopy and understory trees to liberate resources and, therefore, improve growth conditions of the released residual trees (Smith et al. 1997). Accordingly, growth rates of residual trees following partial harvest have increased in trees of different species and ages (e.g., Drew and Flewelling 1979, Bodner 1984, Kneeshaw et al. 2002, Jones and Thomas 2004).

Partial harvest causes higher growth rates of residual canopy trees through increases in light interception of exposed tree crowns (Wyckoff and Clark 2005) whose lower-canopy leaves adjust to higher maximum area-based photosynthetic rates and higher stomatal conductance (Jones and Thomas 2007). .Hence, increases in light interception increase photosynthetic rates but also increase water demand for transpiration.

Residual trees close to skid trails may also experience root damage (Rönnberg 2000, Ouimet *et al.* 2005) and soil compaction (Kozlowski 1999) and this may impair root development (Taylor & Brar 1991). Lower water availability in compacted soils (Starsev & McNabb 2001) and decreased water uptake by damaged root systems both reduce the water supply of affected trees. To mitigate the impact of water shortage and drought stress to the whole organism trees can down regulate their transpiration rates by decreasing their canopy leaf area or by reducing the stomatal conductance of their canopy (Sperry 2000, Sperry et al. 2002).

Experimental studies of tree physiological responses to stand thinning are often limited to few measurements and 1 – 2 growing seasons only (e.g. Bréda et al. 1995, Stoneman et al. 1997, Jones and Thomas 2007). Instead, tree-rings provide an integrated archive of the environmental conditions at the time when the wood was deposited (Saurer et al. 1997). They can serve to trace back the growth responses but also the photosynthetic behavior of trees for thousands of years with an annual resolution (McCarrol and Loader 2004). Fluctuations in stable carbon isotope ratios of tree-rings have been used to reconstruct past climate conditions (e.g. Lipp et al. 1991) but also in ecophysiological studies relating climatic variables to physiological processes such as respiration (e.g. Berninger et al. 2000, Bowling et al. 2002&2003, Fessenden and Ehleringer 2003).

However, variations in $\delta^{13}C$ can also be caused by increases in photosynthetic activity at constant stomatal conductance. Scheidegger et al. (2000) used information on evaporative enrichment in the $\delta^{18}O$ of plant matter to distinguish between biochemical and stomatal limitations to photosynthesis in response to changes in environmental conditions (e.g., precipitation). Saurer et al. (1997) proposed linking growth rates with variations in $\delta^{13}C$ to indicate whether photosynthetic activity or stomatal conductance caused variations in $\delta^{13}C$ in response to environmental conditions: (1) If enhanced photosynthetic activity at constant stomatal conductance (= no water stress) increases $\delta^{13}C$ growth rates should increase simultaneously. (2) If increased stomatal conductance (= decreasing water stress) increases CO_2 supply, $\delta^{13}C$ becomes more negative along with higher growth rates indicating higher photosynthetic activity. (3) $\delta^{13}C$ may stay constant if the plant controls stomatal conductance and photosynthetic capacity simultaneously. In this situation growth rates may vary depending on the tree's ability to adjust to prevailing growth conditions (i.e. irradiance, water supply). Similarly, a constant photosynthetic rate under reduced stomatal conductance (due to reduced water supply) will yield higher $\delta^{13}C$ and lower growth rates.

In this study, we investigated the responses of radial growth rates and stable carbon isotope discrimination in stem wood of residual sugar maple trees (*Acer saccharum* Marsh.) following partial harvest. Trees were classified according to the degree of impact (soil disturbance, light increases) from harvest. To interpret changes in radial growth and ^{13}C discrimination in response to harvest disturbance the application of the theoretical framework of Saurer et al. (1997) allowed us to formulate the following hypotheses (*sensu* Saurer et al. 1997): (1) completely undisturbed trees (no light increase, no soil disturbance) should show no significant changes in neither growth rates nor $\delta^{13}C$ following harvest (constant photosynthetic rate at constant stomatal conductance and no water stress); (2) trees with strongly increased light levels but with no soil disturbance should show higher growth rates and less negative $\delta^{13}C$ values following harvest; (3) trees with no increase in light levels but with much soil disturbance should have constant (or decreasing) growth rates and less negative $\delta^{13}C$ values following harvest, and (4) trees with strongly increased light levels and with much soil disturbance should have decreased growth levels and much less negative $\delta^{13}C$ values following harvest.

4.4 Material & methods

STUDY SITE

The study sites are located in western Quebec (Canada, 46°43' north, 79°04' west). The region has a mean annual temperature varying from 2.5 to 5.0°C, the growing season extents over 170 to 180 days and the mean annual precipitation ranges from 800 to 1000 mm, with snowfall comprising roughly 25% of total precipitation (Gosselin et al. 2000). Soils are podzols with sandy to loamy texture derived principally from glacial tills or fluvio-glacial deposits (Robitaille and Saucier 1998).

STUDY PLOTS

In 2004 and 2005, 19 plots (26 m x 56 m) were established in sugar maple stands on level ground or on gentle slopes with good to moderate drainage. In 1988 the stands had experienced a severe forest tent caterpillar (*Malacosoma disstria* Hubner, FTC) outbreak and had been harvested by selection cuts in 1993 or 1994 which reduced pre-harvest basal area from an average 27 m^2/ha to an average 21 m^2/ha.

In the plots, sugar maple was, on average, the most frequent species (almost 70% of total basal area), followed by yellow birch (*Betula alleghaniensis* Britton, 18%), red oak (*Quercus rubra* L., 3.0%). American beech (*Fagus grandifolia* Ehrh., 2.3%), eastern hemlock (*Tsuga canadensis* [L.] Carr., 1.8%), eastern white cedar (*Thuja occidentalis* L., 1.6%), and red maple (*Acer rubrum* L., 1.5%). Other species, such as balsam fir [*Abies balsamea* (L.) P. Mill.] and white spruce [*Picea glauca* (Moench) Voss], occurred in minor proportions ($\leq$ 1% of total basal area) (Table 4.1). Average post-harvest diameter at breast height (*dbh*, 1.3 m above ground) varied between 155 mm for balsam fir and 422 mm for eastern hemlock. Canopy height reached 19.2 m in eastern white cedar and up to 23.8 m in red oak (Table 4.1).

Table 4.1
Minimum, maximum and mean tree diameter at breast height (*dbh*, mm) and tree height (m) and average tree density per species in the sample plots

	Tree *dbh* (mm)			Tree height (m)			Average density	
Species	min	max	mean	min	max	mean	(tree/ha)	m^2/ha
Yellow birch	92	849	271	5.8	31.1	19.3	49	18.0
Red oak	91	685	405	11.2	30.8	23.8	4	3.0
White spruce	91	370	196	6.1	25.7	15.2	6	0.9
Red maple	93	720	299	7.1	33.3	21.9	3	1.5
Sugar maple	91	792	230	5.3	35.8	18.3	269	69.9
American Beech	91	542	203	4.9	31.0	15.4	11	2.3
Eastern hemlock	225	631	422	14.9	24.3	20.1	3	1.8
Balsam fir	91	270	155	6.1	19.6	12.4	10	1.0
Eastern white cedar	173	575	416	2.5	26.4	19.2	2	1.6

Within the plots, the diameter of all live and dead trees >9.1 cm *dbh* and of all stumps (dsh, ≈ 0.5 m above ground) from the 1993/1994 harvest was measured and their position was mapped. We achieved mapping by laying out a virtual grid on the forest floor for which the plot center line served as y-coordinate. X-coordinates were determined by measuring (using a Hägloff Vertex III® hypsometer, Haglöf Sweden AB) the perpendicular distances of tree positions from the center line. Orientation (magnetic azimuth) of the plot center line was measured with a standard forester's compass.

Skidding trails from the 1993/1994 harvest were also measured. However because regeneration dynamics and litter accumulation since harvest (≈ 11 years) made skidding trail identification difficult, we used several indicators as evidence: (1) linear opening in the canopy, (2) ruts and tire (or skidding) wounds at the basis of trees, (3) dense undergrowth of light and soil disturbance-dependent species (e.g. yellow birch, pin cherry [*Prunus pensylvanica* L.f.], poplars [*Populus* spp.]), (4) stumps in the proximity, (5) absence of obstacles (boulders, escarpments etc.), (6) conformity with machinery constraints (e.g. turning radius), and (7) general concordance with the trail network and stand features. Only when all of these criteria were satisfied, skidding trails were considered for further analysis.

We drew the skidding trail paths as the estimated center of skidding trails on the tree maps using tree positions as landmarks. We could not directly measure trail width because of forest floor vegetation and litter accumulation. We therefore estimated original trail width

with an approximate but realistic machinery width (4 m). Hence, skidding trails were assumed to be 2 m wide from either side of the central trail path.

We evaluated the impact of machinery traffic on soil bulk density by measuring penetration resistance with a dynamic penetrometer (PEM-1, Roctest Inc., Montreal, Quebec). In each of the plots, we took five measurements at ~1 m intervals across each three transects on skidding trails and three on the undisturbed forest floor. For trail measurements we selected only trail sections with clearly defined trail features (wheel tracks, inter-wheel space, off trail). Transect locations were chosen randomly and the five measurements on skid trails were placed so that measurement 1 and 5 were off-trail, measurement 2 and 4 on wheel tracks, and measurement 3 in the inter-wheel space.

TREE-RING DATA

In the mapped plots increment cores (3 cores per tree) were taken of all trees between 19.1 cm and 49.0 cm *dbh* as a retrospective measure of radial growth. Trees <19.1 cm were not sampled to avoid the juvenile effect in ^{13}C discrimination (Freyer 1979, Francey and Farquhar 1982) and to avoid trees with heavily suppressed growth rates. Trees >49.0 cm were not sampled to avoid trees with declining growth rates due to senescence. We sampled a total of 321 sugar maple trees.

Increment cores were progressively sanded down to grain 400 to allow unambiguous identification of tree-rings. We measured tree-rings with a microscope equipped with a computer-assisted micrometer (0.001 mm precision). At least two cores per tree were readable in most cases and we averaged ring-width measurements among cores to account for intra-tree variability of radial increment due to growing conditions or leaning (Kienholz 1930, Peterson and Peterson 1995). This then yielded a single growth chronology per tree.

We took radial growth measurements of dominant canopy trees to construct a master chronology by adding progressively highly correlated (r-values ≥0.3, Tardif et al. (2001)) tree-ring series to the already existing ones and obtained a final master chronology containing 29 individual tree-ring series with an overall cross-correlation coefficient of 0.479.

We cross-dated (matching of tree-rings with calendar years) the remaining tree-ring series based on (1) visual examination of marker years (severe growth declines in 1971 and 1988) and (2) cross-correlation coefficients of chronology segments with the master chronology. We ran COFECHA to detect missing or false rings in individual segments of tree-ring series and, in suspect cases, we identified false or missing rings on the cores or cross sections and added tree-rings with zero width or removed these from the series. We then run COFECHA again on theses series to verify improvements of the cross-correlations with the master chronology.

Only trees whose ring-width series showed strong cross-correlations ($r > 0.4$) with the master chronology were retained for further analysis. Because we wanted to exclude harvest disturbance not related to sudden light increases or soil disturbance from influencing growth and carbon isotope responses, we withheld data from trees with obvious and severe mechanical damages from harvest (uprooting, bole breakage, etc.) from further analysis.

We standardized these tree-ring series by dividing each individual tree-ring series by its long-term growth trend, estimated with a cubic smoothing spline over the entire series. Resulting dimensionless ring-width indices could be more adequately compared among trees at different ages and from different sites. This standardization procedure was done using the i.detrend function from the contributed R package dplR (Bunn 2007) in the R software environment for statistical computing and graphics (version 2.6.0, R Development Core Team 2007).

Because stable carbon analysis was limited to the period 1983 – 2003 (see below) the growth series were truncated for further analysis at these years. In order to reduce inter-tree differences in ring-width indices before harvest we rescaled each series individually by dividing each ring-width series by its pre-harvest (1983-1993) average. These rescaled values could be more adequately compared and averaged over treatment groups than series of raw ring-width indices.

MEASURES OF HARVEST DISTURBANCE

Sudden changes in light conditions

Because the harvest took place 11 years prior to sampling, changes in light conditions could not be measured directly and had to be estimated retrospectively. Using spatial information on trees and stumps of the last harvest, we were able to simulate pre-harvest stand conditions. To achieve this, we converted dsh measurements of tree stumps to *dbh* with existing conversion tables (MRNFP 2003) and these were then considered *dbh* measurements of cut trees before harvest. When external criteria of dead trees such as the presence of bark and fine branches, stem wood decay or crown deterioration (Sénécal et al. 2003) indicated that these trees died only after harvest we considered these trees as being alive in the pre-harvest stands (2.9% of all trees). The *dbh* measurements and estimates of all trees present before harvest (live trees + cut trees + trees dead ≤11 years) were then loaded into the forest dynamics simulator SORTIE to estimate light availability for individual trees (a comprehensive overview of SORTIE's structure and simulation procedure can be found in Deutschman *et al.* (1997) at: http://www.sciencemag.org/feature/data/deutschman/index.htm).

We parameterized SORTIE with regional parameters of tree species allometry and tree canopy light extinction coefficients (Lefrançois et al., in press). Based on these parameters, SORTIE models tree dimensions and estimates light availability for each individual tree in the stand as the seasonally averaged percentage of full sun (Canham 1988). Estimations of light availability for each individual tree, in the centre of simulated crowns at 0.75*crown height, were done for pre- and post-harvest plots. Dividing post-harvest light availability by pre-harvest light availability yielded our measure of changes in light conditions.

Soil disturbance at tree proximity

Assuming that tree crown dimensions can be predicted from tree diameter, and that tree crown dimensions are a proxy for tree root system coverage (Tubbs 1977), a circular 'influence zone' was estimated around each tree based on species specific parameters of diameter-crown relationships. This yielded a diameter-dependent influence zones with radii (m) for sugar maple = 0.100**dbh* (cm) (Beaudet *et al.* 2002). By intersecting the influence zones of the mapped trees with the mapped skidding trails we obtained an estimate of the

proportion of the influence zone that had been disturbed by machinery traffic. The ratio of the area of the influence zone disturbed by machinery traffic divided by the total area of the influence zone served as our measure of soil disturbance at tree proximity.

Disturbance classes

All retained trees were grouped into 4 disturbance classes: (1) trees without sudden increases in light levels or soil disturbance (no disturbance treatment), (2) trees with strong sudden increases (>100%) in light levels following harvest but without soil disturbance (light treatment); (3) trees with no sudden increase in light levels but with soil disturbance (>30% of influence zone (soil treatment), and (4) trees with both strong sudden increase (>100%) in light levels following harvest and with soil disturbance (>30% of influence zone (light and soil treatment). For each of the 4 disturbance classes we selected randomly 5 trees for both growth and stable carbon isotope analysis. Sample sizes were limited because of the large number of carbon isotope analysis (20 trees x 21 years = 420 analyses) and associated costs.

The threshold for soil disturbance for these four classes had been set assuming that disturbance >30% of the forest floor surrounding trees should have an affect on tree growth and water status through the impact of soil compaction and root damage (Kozlowski 1999, Rönnberg 2000, Ouimet *et al.* 2005). For sudden increases in light levels we chose >100% because increases up to ~40% have been found to still allow a gradual acclimation of leaf-level photosynthetic activity in mature sugar maple trees (Jones and Thomas 2007).

STABLE CARBON ISOTOPE ANALYSIS

The isotopic composition of a carbon compound ($\delta^{13}C$), the proportional deviation of the $^{13}C/^{12}C$ ratio from the Vienna Peedee belemnite (VPDB) carbonate standard is defined as:

$$\delta^{13}C = \left(\frac{^{13}C/^{12}C_{Sample}}{^{13}C/^{12}C_{VPDB}} - 1 \right) \times 1000‰ \quad (1)$$

In plant organic matter the $^{13}C/^{12}C$ ratio (δ_p) is depleted in ^{13}C compared to the atmospheric ^{13}C composition (δ_a). This discrimination (Δ) against ^{13}C can be expressed as:

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p} \tag{2}$$

Discrimination of ^{13}C over ^{12}C results from two processes. Firstly, $^{13}CO_2$ diffuses more slowly in air (and thus through stomata) into the intercellular spaces of the leaves due to its heavier molecular mass. Secondly, the enzyme-catalyzed fixation of CO_2 itself (Rubisco carboxylation) causes a further discrimination against $^{13}CO_2$. Considering only C_3 plants (as all trees are), we can express the fractionation process as follows (Farquhar et al. 1989):

$$\Delta = a\frac{p_a - p_i}{p_a} + b\frac{p_i}{p_a} = a + (b - a)\frac{p_i}{p_a} \tag{3}$$

where Δ is the ^{13}C discrimination and a and b are the parameters describing, respectively, the fractionation due to diffusion of CO_2 in air (4.4‰, a theoretical value) and by the enzyme Rubisco (22‰ to 34‰). The parameters p_a and p_i represent partial pressures of CO_2 in the ambient air and the intercellular air spaces, respectively.

The trees selected for further analysis were cut down and cross sections of the trunk were taken at 1.3 m height. To avoid carbon contamination from chain saw lubricants small rectangular pieces were cut from the interior of these cross sections with a band saw. The sections were then further cut to cover a 10-year period before and after the year of harvest which yielded a sampling period spanning from 1983 to 2003.

Although the actual fractionation processes of the heavier $^{13}CO_2$ are beyond active control by plants p_i inside the leaf is influenced by stomatal aperture as follows. Under conditions of limited water supply, plants reduce the leaf stomatal conductance through partial or complete stomata closure in an attempt to use water more efficiently, i.e. to fix more carbon for each unit of water transpired. Since stomata closure also limits diffusion of CO_2 into the leaf, the intercellular concentration of CO_2 drops with continued photosynthesis. From equation (3) it is obvious that this will decrease Δ. Hence, higher water use efficiency is therefore associated with decreases in Δ (Farquhar and Richards 1984) and this makes stable carbon isotope ratios a useful measure for plant water relations (Francey and Farquhar 1982, Farquhar et al. 1989).

To prevent mobile substances and handling contaminations from interfering with stable carbon isotope measurements the wood sections were extracted with a 2:1 (v/v) toluene:methanol solution for several hours in a heated ultrasonic bath and oven-dried at 70°C overnight (Loader et al. 1997). Single tree-rings were then shaved from the wood sections with a surgical scalpel. These shavings were milled in a ball mixer mill MM 200® (Retsch GmbH, Haan, Germany) to ascertain a homogeneous distribution of late and early wood in the sample. Three of the wood section had tree-rings so tightly spaced that shaving with annual precision and subsequent milling was not feasible. These sections were therefore cut to dimensions that allowed their measurement in a 'laser ablation combustion gas chromatography isotope ratio mass spectrometry' (LA-C-GC-IRMS) (Schulze et al. 2004). All other milled wood samples were weighted in tin cups and processed with a conventional 'elemental analyzer' (EA)-IRMS. Since the laser ablation technique necessitated the use of whole wood sections, conventional isotope ratio analysis was also based on whole wood samples. Moreover, it has been shown by others that undecayed whole wood and extracted cellulose had very coherent $\delta^{13}C$ signatures with whole wood samples having slightly less negative $\delta^{13}C$ values (Loader et al. 2003). Laser trajectories spanned across the entire ring width so that ablated wood material contained both early and late wood and that averaged $\delta^{13}C$ values could be considered representative for entire tree-rings.

Sequential isotopic analyses of milled wood samples were done using a Finnigan MAT DeltaPlus XL EA-IRMS coupled to an autosampler. For the laser ablation technique a frequency quadrupled Nd:YAG 266 nm UV-laser (New Wave Research Merchantek) was used for ablating wood dust from the samples. After combustion of the ablated wood dust CO_2 was separated from other combustion gases and analyzed with a Finnigan DeltaPlus XL EA-IRMS. Measurement precision of $\delta^{13}C$ analyses was $< 0.1‰$ for milled wood samples and $< 0.25‰$ for the laser ablation technique, based on measurements of an internal lab standard (NBS 22: -30.03‰ vs. VPDB scale). All isotope measurements were done in the Iso-Lab of the Max-Planck-Institute for Biogeochemistry in Jena.

For consistency with ring-width measurements and to reduce differences in $\delta^{13}C$ between individual trees, we rescaled $\delta^{13}C$ values by dividing individual time series by their pre-harvest (1983-1993) average. This rescaling implies that values below 1 are indicative of

post-harvest increases in $\delta^{13}C$ (less negative) and are therefore indicative of constrained post-harvest water status. Values above 1 indicate improvements in water supply or decreases in water use and are therefore indicative of releases of the pre-harvest water status of trees.

We did not correct $\delta^{13}C$ values for time trends due to CO_2 enrichment of the atmosphere because time series spanned across 21 years only and comparisons were undertaken between treatment groups for which the atmospheric enrichment was identical.

CLIMATE-GROWTH AND CLIMATE-$\delta^{13}C$ RELATIONSHIPS

Monthly mean climate data (precipitation, temperature) were obtained from the Canadian National Climate Data and Information Archive, operated and maintained by Environment Canada (http://climate.weatheroffice.ec.gc.ca). Weather stations closest to our study sites (~ 60 km) were Barrage Temiscaming (46° 42.600' N, 79° 6.000' W, elevation 181.40 m) and Rapide des Joachims (46° 12.000' N, 77° 42.000' W elevation 137.20 m). Monthly climate data from Barrage Temiscaming were discontinued from 1995 onwards so we amended the data set by adding data from Rapide des Joachims and averaged values in overlapping years (1983-1995).

To quantify the climate–growth and the climate-$\delta^{13}C$ relationships, we performed a correlation and response function analyses with the program Dendroclim2002 (Biondi and Waikul, 2004). The correlation function gives univariate estimates of Pearson's product moment correlation between ring-width indices (or $\delta^{13}C$ indices) and climate variables, whereas the response function is a principal component regression model of the multivariate climate data with ring-width indices (or $\delta^{13}C$ indices) as the response variable. To account for multicollinearity in climate data and to add more accuracy to the correlation and the response function analysis, Dendroclim2002 computes bootstrapped confidence intervals of the parameter estimates for both functions (Biondi and Waikul, 2004). Only climate variables with consistently positive or negative parameter estimates within the 95% bootstrapped confidence interval are considered significant.

STATISTICAL ANALYSIS

We tested for differences of rescaled ring-width indices and of rescaled $\delta^{13}C$ between treatments on an annual basis. Due to small sample sizes (5 trees per treatment for 4 treatments per year = 20 measurements per year) and because of heteroscedasticity of the variances among groups we avoided the use of ANOVA. Instead we used a permutational analysis of variance (Anderson 2001, McArdle and Anderson 2001) with the free statistical program PERMANOVA (Anderson 2005). PERMANOVA tests assume only that individual observations can be exchanged under a true null hypothesis. The program provides a partitioning of variation, based on distance measures, according to treatment factors and uses permutations to test for differences between groups (factor levels). First, the program estimates a distribution of the test statistic F under a true null hypothesis (i.e., no differences between groups) by randomly shuffling group labels among observations. For each permutation PERMANOVA computes the test statistic F^*. Probabilities for the tests under a true null hypothesis are computed as the proportion of all permutational F^* values that are greater than or equal to the value of F observed for the real data (Anderson 2005). Similarly, pairwise comparisons are based on the permutational test statistic t^* and probabilities for the test under a true null hypothesis are estimated as the proportion of all permutational t^* values that are greater than or equal to the value of t observed for the real data.

For both test procedures we used 4999 permutations to estimate F^* and t^* distributions as recommended by the authors of the program (Anderson 2005). Significance levels of permutational ANOVA was 0.05 but were adjusted for multiple comparisons using the Tukey correction which, for six comparisons, yields an α threshold of 0.0085.

We used contrasts of pre- vs. post-harvest levels in rescaled ring-width indices and in rescaled $\delta^{13}C$ within treatments to test whether harvest caused a change in these variables within a given treatment. Significance tests of these contrasts were done with t-tests after confirming normality of the sample distributions with Kolmogorov-Smirnov tests.

4.5 Results

Average breast-height diameters ranged from 241 mm (light & soil treatment) to 379 mm (soil treatment). Trees within the light treatment (n = 5) had a mean light increase of more than 10 times the preharvest light availability. Mean soil disturbance of trees within the soil treatment (n = 5) was 48.2% of the tree's influence zone whereas for trees that experienced also increases in light levels (n = 5) mean soil disturbance was 46.1% with an average light increase of 9.55 times preharvest light availability (Table 4.2).

Table 4.2
Mean diameter (mm), soil disturbance (%), light change ratio, height (m), and sample size (n) of trees in the four disturbance classes. Values in parenthesis are minima and maxima. Light change ratios are light availability after harvest/before harvest; a value of one indicates no change in light availability

	Disturbance class			
	No	Light	Light & soil	Soil
Dbh (mm)	310 (215-456)	282 (237-360)	241 (197-337)	379 (344-410)
Soil disturbance (%)	0 -	0 -	46.1 (31.3-68.4)	48.2 (37.0-52.6)
Light change ratio	1 -	10.61 (2.52-26.29)	9.55 (2.13-16.81)	1 -
Height (m)	22.36 (17.2-25.8)	19.4 (16.9-23.4)	18.1 (13.5-22.2)	22.4 (18.1-29.5)
Sample size (n)	5	5	5	5

Ring-width indices showed a marked decline across all disturbance classes in 1988, the year of the FTC outbreak (Fig. 4.1, upper panel). Pre-harvest growth levels in the 'no disturbance' treatment were higher than that of other disturbance classes especially in the period following the insect outbreak. Growth rates increased after harvest in all treatments but only briefly so for the 'no disturbance' treatment. These growth increases levelled off by 2001 (Fig. 4.1, upper panel). $\delta^{13}C$ showed some increase in 1988 in all but the 'soil' treatment (Fig. 4.1, lower panel). From 1988 to 1990, $\delta^{13}C$ declined and then increased until 1993/1994 in all treatments. From 1994 onwards $\delta^{13}C$ either declined ('light' and 'soil'

treatment) or remained constant ('no' and 'light & soil' treatment) over time until 2003 (Fig. 4.1, lower panel).

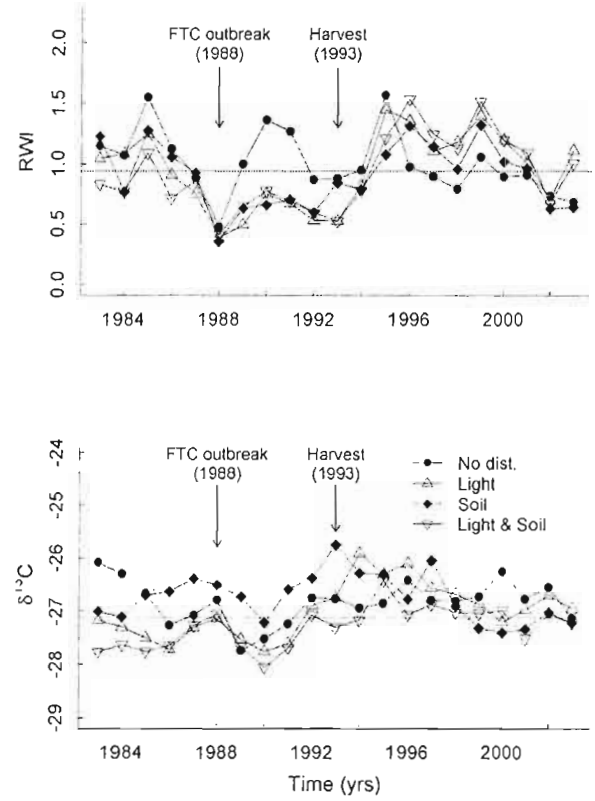

Figure 4.1 Average ring-width indices (upper panel) and average $\delta^{13}C$ (lower panel) from 1983 – 2003 of the four disturbance classes. The horizontal lines indicate the pooled average of all 1983-2003 values. Note the negative impact of the forest tent caterpillar (FTC) outbreak on ring-width indices of all disturbance classes.

Rescaled ring-width indices showed two declines within the 1983-2003 period dropping below the pooled (all treatments) pre-harvest average. In 1988, the year of the FTC outbreak rescaled growth indices of all disturbance treatments declined below the 1983-1993 average (Fig. 4.2, upper panel). However, trees of different disturbance classes responded differently to harvest. Mean rescaled ring-width indices of trees in the 'light' and in the 'light & soil'

treatment increased and stayed above pre-harvest levels until 2003 (except for 2002 where the 'light' treatment fell briefly and slightly below the mean). Mean rescaled ring-width indices of the 'soil' treatment showed a one-year lag in response but increased in 1995 and stayed above pre-harvest mean until 2002. 'No disturbance' trees showed only a brief increase in 1995 but fell below the pre-harvest mean right after and remained there until 2003 (Fig. 4.2, upper panel). Standard deviations of rescaled ring-width indices increased from harvest onwards and were similar among trees in the 'no', 'light', and 'soil' treatment but were highest in the 'light & soil' treatment (Fig. 4.2, lower panel).

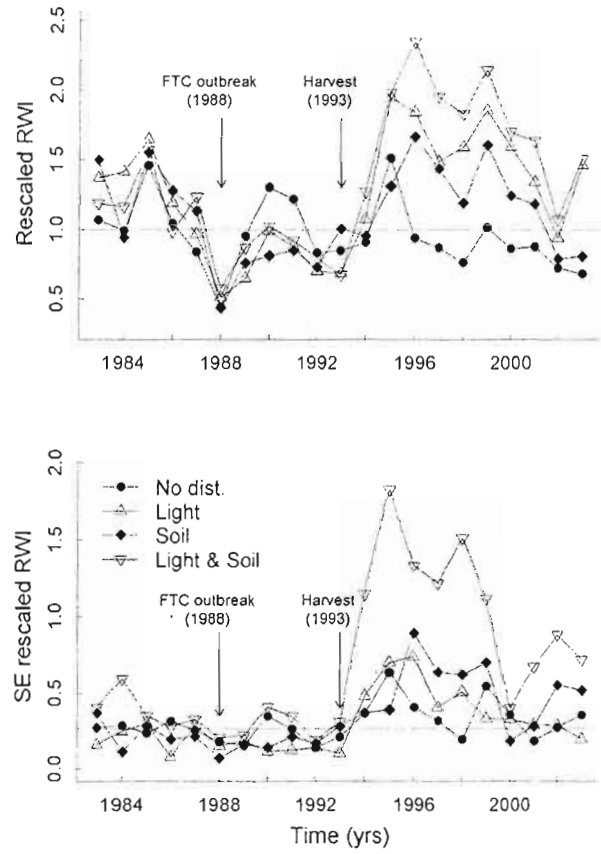

Figure 4.2 Average rescaled ring-width indices (upper panel) and standard errors of rescaled ring-width indices (lower panel) from 1983 – 2003 of the four disturbance classes. The horizontal lines indicate the pooled average of all rescaled pre-harvest (1983-1993) ring-width indices or standard errors. Note the negative impact of the forest tent caterpillar (FTC) outbreak on standardized ring-width of all disturbance classes.

From 1993 onwards, rescaled $\delta^{13}C$ stayed below the pre-harvest mean for all disturbance classes but the 'soil' treatment for which they increased above the pre-harvest mean from 1998 onwards (Fig. 4.3, upper panel). Below-average levels in rescaled $\delta^{13}C$ are equivalent to post-harvest increases $\delta^{13}C$ (i.e. less negative) relative to pre-harvest levels and are therefore indicative of water stress. Thus average rescaled post-harvest $\delta^{13}C$ are indicative of water stress in the 'light' and 'light & soil' treatment until 1998 which then levelled off. Rescaled post-harvest $\delta^{13}C$ of the 'no' treatment were quite stationary throughout the period and the

'soil' treatment even showed increases (i.e. release of water stress) from 1998 onwards. Standard errors of rescaled $\delta^{13}C$ are generally higher in the post-harvest period except for the soil treatment for which standard errors were higher at the beginning and at the end of the 1983-2003 period and lower in between (Fig. 4.3, lower panel).

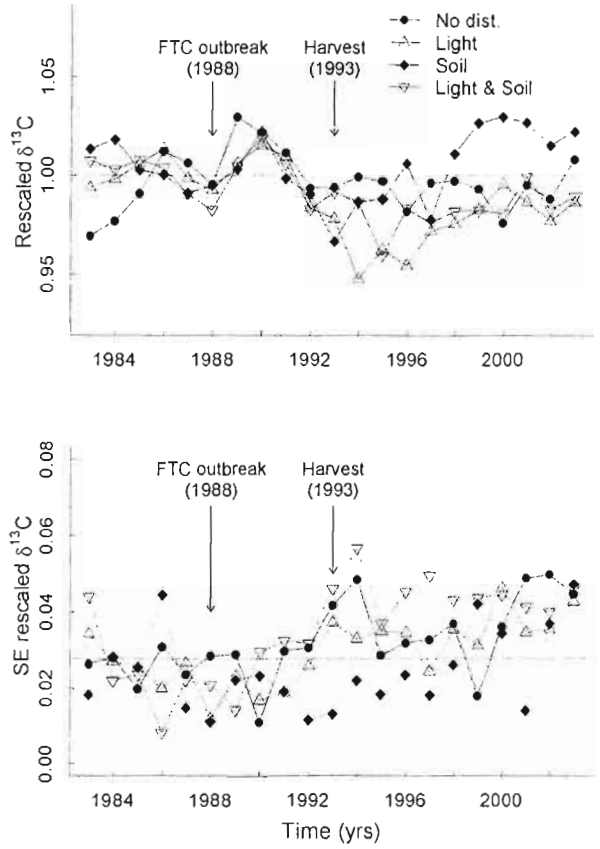

Figure 4.3 Average rescaled $\delta^{13}C$ (upper panel) and standard errors of $\delta^{13}C$ (lower panel) from 1983 – 2003 of the four disturbance classes. The horizontal lines indicate pooled average (all disturbance classes) of rescaled pre-harvest (1983-1993) $\delta^{13}C$.

Summer precipitation was quite variable in the study region throughout the period 1910-2003 with a long-term mean of 78.10 mm. Most abundant mean summer precipitation was received in 1970 and the driest summer was in 1975 (Fig. 4.4). During the period of growth

and $\delta^{13}C$ sampling (1983-2003), the forests received a maximum of almost 120 mm of precipitation per summer month in 1984 and monthly mean summer precipitation was lower than averages in 1987, 1989, 1999, and 2001, and lowest in 2002 (Fig. 4.4). Average monthly mean summer temperature was above the long-term mean (13.65°C) for almost the entire 1983-2003 period except in 1984 and 1992. However, in the years following partial harvest monthly mean summer temperatures were very close to the long-term mean (Fig. 4.4).

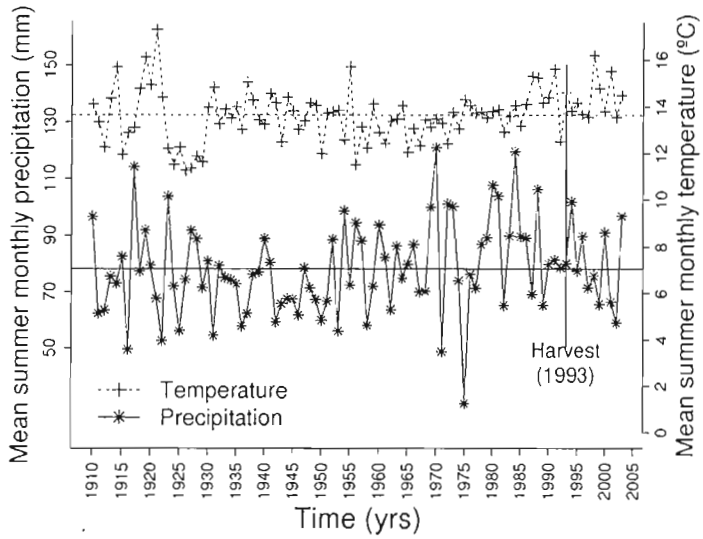

Figure 4.4 Mean monthly summer (April-August) precipitation (solid line with stars) and temperature (dotted line with crosses) computed from climate data covering the years 1910-2003. Horizontal lines indicate the long-term mean precipitation and temperature across these years. Vertical lines indicate the year of the beginning of the growth and $\delta^{13}C$ sampling period (1983) and the year of the partial harvest (1993).

Climate-growth relationships of trees were quite similar across disturbances classes (Fig. 4.5). Both correlation and response function coefficients showed a similar pattern in current year's precipitation although the significant positive correlation of July precipitation with growth in the 'no disturbance' treatment was not significant in other treatments. Surprisingly, August precipitation was negatively correlated to growth and had significant regression parameters in the 'no disturbance' and the 'soil' treatment. This tendency also showed in the

other treatments but coefficients were not significant. Prior fall and winter (November and January) precipitation had a positive influence on growth in the 'no' treatment but not in the other treatments for which prior October precipitation had a negative influence on growth (Fig. 4.5, left panel). Prior October temperature had a significant positive effect on growth of all disturbance classes and June temperature was positively correlated with growth in the 'light' and 'light & soil' treatment (Fig. 4.5, right panel).

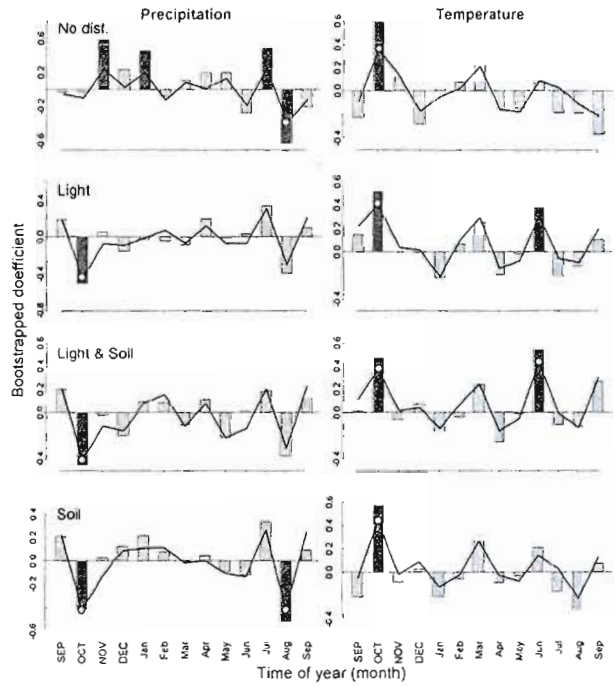

Figure 4.5 Correlation (bars) and response function (lines) analysis of rescaled ring-width indices and climate data. Monthly precipitation (left) and temperature (right) from prior (upper case) September to current (lower case) September (1983-1994) were used to explain variance in rescaled ring-width indices of trees in the four disturbance classes. Significant correlation and response function coefficients ($P<0.05$) are indicated with dark grey bars and white circles, respectively.

Climate-$\delta^{13}C$ relationships were less obvious. No clear pattern established for precipitation correlation or regression coefficients in the 'no disturbance' treatment (Fig. 4.6). Although one would expect rescaled $\delta^{13}C$ values to be consistently positively correlated to

any form of precipitation (i.e. precipitation causes post-harvest $\delta^{13}C$ to be lower, more negative than the pre-harvest mean) this was not necessarily the case. Although winter (December) and spring (March) precipitation were positively correlated with rescaled $\delta^{13}C$ in the 'light' treatment and summer (June) precipitation in the 'soil' treatment no significant relationship could be detected in the 'light & soil' treatment (Fig. 4.6, left panel). Temperature was not correlated with rescaled $\delta^{13}C$ in the 'no disturbance' treatment. In the 'light & soil' and the 'soil' treatment December temperatures were negatively correlated with rescaled $\delta^{13}C$ and had significant regression parameters whereas June temperatures were negatively correlated with rescaled $\delta^{13}C$ in the 'light' treatment. On the other hand February temperature was positively correlated with rescaled $\delta^{13}C$ in the 'light' and the 'soil' treatment and April temperature in the 'light' and 'light & soil' treatment (Fig. 4.6, right panel).

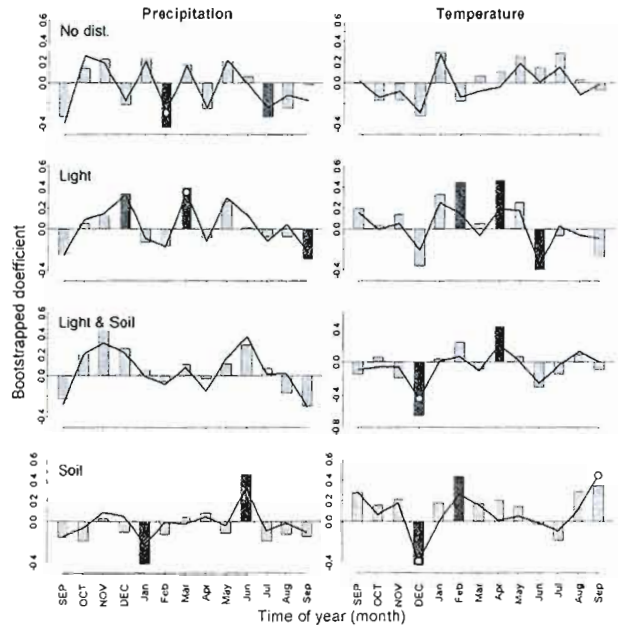

Figure 4.6 Correlation (bars) and response function (lines) analysis of rescaled $\delta^{13}C$ and climate data. Monthly precipitation (left) and temperature (right) from prior (upper case) September to current (lower case) September (1983-1994) were used to explain variance in rescaled $\delta^{13}C$ of trees in the four disturbance classes. Significant correlation and response function coefficients ($P<0.05$) are indicated with dark grey bars and white circles, respectively.

PERMANOVA analysis indicated that rescaled ring-width indices were significantly different between treatments in 2000 ($p = 0.0036$), 2001 ($p = 0.0324$) and 2003 ($p = 0.0302$). Multi-comparisons based on permutation tests in these years were, after Tukey correction, significantly different only between the 'no disturbance' and the 'light' treatment and this only in 2003 ($P = 0.0054$). However, rescaled ring-width indices were also significantly different between the 'no disturbance' and the 'light treatment in 1991 and 1998 (both $P = 0.0054$) even though PERMANOVA did not indicate significant difference overall (Table 4.3). Rescaled $\delta^{13}C$ values were not statistically different in any of these years or in any other years from 1983 to 2003.

Table 4.3
Annual permanova table for years with significant or marginally significant differences in rescaled ring-width indices and multi-comparisons among disturbance treatments with significant differences within these years using permutation tests based on 4999 resamples

							Multiple comparisons L vs. No	
	Source	df	SS	MS	F	*P(perm)*	t	*P(mc)*
1991	dist.class	3	0.4337	0.1446	2.3208	0.1112	2.6129	**0.0054**
	Residual	16	0.9967	0.0623				
	Total	19	1.4304					
1998	dist.class	3	3.2861	1.0954	1.4785	0.2254	3.4097	**0.0054**
	Residual	16	11.8539	0.7409				
	Total	19	15.14					
2000	dist.class	3	2.1691	0.723	6.7271	**0.0036**	3.3896	0.0128
	Residual	16	1.7197	0.1075				
	Total	19	3.8888					
2001	dist.class	3	1.5103	0.5034	3.1188	**0.0324**	3.0287	0.0128
	Residual	16	2.5827	0.1614				
	Total	19	4.0929					
2003	dist.class	3	2.7749	0.925	3.9047	**0.0302**	4.313	**0.0054**
	Residual	16	3.7901	0.2369				
	Total	19	6.565					

Contrasting pre- (1983-1993) vs. post-harvest (1994-2003) levels of rescaled ring-width indices within disturbance classes showed statistically significant increases in growth rates in the 'light' ($P < 0.001$), the 'light & soil' ($P < 0.001$) and in the 'soil' treatment ($p = 0.025$) but not in the 'no disturbance' treatment ($P = 0.256$, Table 4.4). Rescaled $\delta^{13}C$ decreased

significantly in the 'light' ($P < 0.001$) and 'light & soil treatment' ($p = 0.008$) but not in the 'no disturbance' treatment ($p = 0.290$) but increased, albeit not statistically significantly, in the 'soil' treatment ($p = 0.126$, Table 4.4).

Table 4.4
T-tests of differences between post-harvest – pre-harvest levels in rescaled ring-width indices and rescaled $\delta^{13}C$ within treatments

	Rescaled ring-width				Rescaled $\delta^{13}C$			
Treatment	Difference	t	df	p-value	Difference	t	df	p-value
No	-0.085	1.142	95.847	0.256	-0.007	1.0626	96.764	0.290
Light	0.514	-5.678	90.106	<0.001	-0.026	4.239	88.283	<0.001
Light $ Soil	0.745	-4.474	61.367	<0.001	-0.018	2.718	102.335	0 008
Soil	0.219	-2.273	83.575	0.025	0.009	-1.542	92.289	0.126

4.6 Discussion

Our data supports hypothesis one and hypothesis two which state respectively that undisturbed trees would not experience any changes in growth rates or $\delta^{13}C$ and that trees with strongly increased light levels but no soil disturbance would show higher growth rates and less negative $\delta^{13}C$ values following harvest. However, we have to reject hypothesis three that trees with soil disturbance would experience increases in $\delta^{13}C$ and decreases in growth rates as well as hypothesis four, i.e. the 'light & soil' treatment would cause significant decreases in growth rates and significant increases in $\delta^{13}C$ indicating water stress, needs to be rejected.

Growth and stable carbon isotope analysis following partial harvest indicated no negative impact of harvest disturbance on growth rates or on water status of residual sugar maple trees. Rescaled growth indices increased after harvest in all but the 'no disturbance' treatment (Fig. 4.2, Table 4.4) whereas rescaled $\delta^{13}C$ were decreased only with sudden increases in light availability but increased slightly with soil disturbance 5 years after harvest (Fig. 4.3, Table 4.4). Our results indicate that none of the studied disturbances from partial harvest caused water stress in residual sugar maple trees.

We are aware of the potential pitfalls that come with limited sample sizes in factorial analytical designs. Also, we are aware that our light availability estimation using SORTIE implies oversimplifications of the complex canopy structure in uneven-aged deciduous forests. Similarly, our measure of soil disturbance is indirect and relies on several assumptions (e.g., negative impact of machinery traffic on soil bulk density and tree root systems, uniform distribution root systems within influence zones) which are, especially about the distribution of tree root systems, unavoidable in a retrospective study. We estimated the impact of machinery traffic on soil bulk density using penetrometer measurements. Even 11 years after harvest penetration ratios (soil penetration per blow) is significantly lower in wheel tracks and in the inter-wheel space than off-trail or in the undisturbed forest floor (Fig. 4.7) indicating persistence of soil compaction from machinery traffic for at least 11 years.

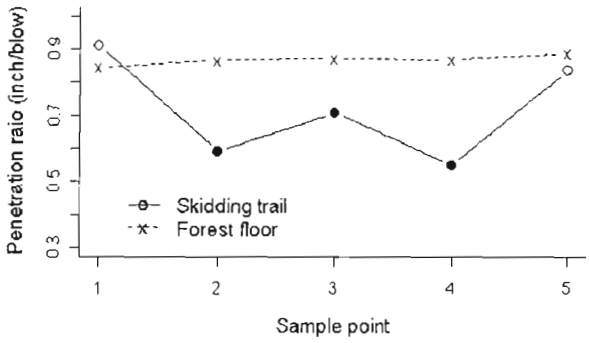

Figure 4.7 Penetration ratios (inch/blow) as an estimate of soil compaction, taken 11 years after harvest across skidding trails or on the undisturbed forest floor. Measurement points on skidding trails 1 and 5 were off-trail, points 2 and 4 on wheel tracks, and point 3 on the inter-wheel space. Points 1 through 5 on undisturbed forest floor were spaced at ~1 m equidistance. Filled circles indicate significant differences ($P<0.05$, Wilcoxon rank sum test) between skidding trail and forest floor measurements at a given point.

In addition, our results on growth responses to harvest disturbances are corroborated by findings from Hartmann & Messier (in review) who analyzed the impact of insect defoliation and harvest disturbances on radial growth and survival probabilities of residual sugar maple trees using the same disturbance measures but greater samples sizes per disturbance class. They found that harvest disturbances had either no impact (soil disturbance) or a positive (sudden exposure to higher light levels) impact on growth compared to the control ('no disturbance') treatment (Hartmann & Messier, in review). The observed increases in growth as response to estimated higher light levels corroborate our method of estimating light availability with SORTIE.

In our study, harvest disturbances also did not have a strong influence on the climate-growth relationships except that in all trees affected by harvest disturbance the positive correlation of prior November and prior January precipitation on growth vanished. Instead prior October precipitation was significantly negatively correlated with growth in all but the 'no disturbance' treatment (Fig. 4.5). The positive correlation of current January precipitation with growth may linked to a better protection of fine roots against freezing damage from

higher snow cover (Tierney et al. 2001) but the shift in correlation from prior October and prior November precipitation to current January precipitation is not clear. Several other studies on climate-growth relationship of sugar maple did not detect these correlations (e.g., Ryan & Allen 1994, Yin et al. 1994, He et al. 2005) or did not try to explain causal relationships (Goldblum & Riggs 2005). The absence of correlation between summer precipitation and growth rates may be linked to the humid climate of our research area and variations in summer precipitation may not explain much of the variation in growth rates.

The positive correlation of prior October temperature with growth indices may also be linked to freezing damage. Yin et al. (1994) used regression analysis to identify a 'peak temperature' of the prior average October precipitation on sugar maple growth indices. They argued that temperatures below this peak (6.4°C) may expose trees to frost damage whereas temperatures above this peak may result in high maintenance respiration (Yin et al. 1994) both of which may reduce the amount of carbon reserves for the upcoming season's vernal growth (Wong et al. 2003).

In our study current June temperature was positively correlated with growth indices in the 'light' and the 'light & soil' treatment (Fig. 4.5). The positive correlation of current June temperature with growth seems indicative of favorable growth condition Trees with increased crown exposure from thinning ('light' and 'light & soil' treatment) took advantage of higher irradiance with increased growth rates which was not the case for trees without changes in crown exposure ('no disturbance' and 'soil' treatment).

Although $\delta^{13}C$ variations have been shown to be correlated with climate variables, such as air temperature and precipitation (e.g., Manzany et al. 1980, Saurer et al. 1995, Robertson et al. 1997, Hemming et al. 1998) or with light intensities and radiation (e.g., Smith et al. 1976, Leavitt & Long 1986, Gessler et al. 2001, Jäggi et al. 2002). We did not find a consistent and intuitive pattern in the climate-$\delta^{13}C$ relationship of our data. Summer precipitation should have a strong negative effect on $\delta^{13}C$ (i.e., more precipitation causes more negative $\delta^{13}C$ values, in our case causing higher rescaled $\delta^{13}C$ indices) but this was not the case in our study, not even in trees with increased light availability ('light' and 'light & soil' treatment) or with assumed reduced water availability/uptake ('soil' treatment).

McDowell et al. (2003) observed that carbon isotope discrimination increased in *Pinus ponderosa* (C. Lawson) following stand thinning through increases in water availability. Maximum discrimination took place only 6 years after thinning (McDowell et al. 2003). It is possible that post-harvest decreases in rescaled sugar maple $\delta^{13}C$ in the 'light' and 'light & soil' treatment were mitigated by increases in water availability through thinning so that no differences could have been detected between treatments in individual years immediately after harvest. Also, Vesala et al. (2005) did not find much influence of thinning on the transpiration of pine trees. Abundant growing season precipitation and moderate summer temperatures in the immediate post-harvest period (1994-1996) could have intensified this effect and may have contributed to further mitigating $\delta^{13}C$ responses to disturbance.

The absence of response in $\delta^{13}C$ to the 'soil' treatment may be explained by an interplay of root turnover and, again, favourable growth conditions. Fine root turnover rates in northern hardwoods have been estimated to be ~8 mo in the uppermost soil layer (<30 cm) and 5.5 mo in deeper soil horizons (>30 cm, Hendrick & Pregitzer 1992). Considering the stimulating effect of root pruning on root growth (Geisler & Feree 1984, Hipps et al. 1999), potential root damage from machinery traffic may have accelerated the replacement of damaged roots. Abundant precipitation during the post-harvest period and rapid root replacement following disturbance may have mitigated water deficits of trees with soil disturbance and thereby prevented substantial increases in $\delta^{13}C$ (i.e. significant decreases in rescaled $\delta^{13}C$).

Interestingly, $\delta^{13}C$ increased in 1988 (Fig. 4.1) despite abundant summer precipitation (Fig. 4.4). The forest tent caterpillar outbreak reached its climax in 1988 and reallocation of reserves for refoliation of defoliated crowns may have caused this increase. Starch reserves stored in woody tissue during winter are enriched in ^{13}C compared to other synthates such as sucrose and hexoses and their mobilization during heterotrophic leaf development in spring has been found to cause increases in stem wood $\delta^{13}C$ (Helle & Schleser 2004). Similarly, refoliation following herbivory predation should have the same effect on $\delta^{13}C$.

4.7 Conclusions

Our results indicate that the redistribution of resources for individual trees following partial harvest is balanced, i.e. increases in water availability through thinning outweigh higher water demands from higher light interception. This may counteract potential decreases in water availability/uptake from soil compaction or root damage, respectively, and prevent a water deficit in affected trees. However, it should be noted that average growing season precipitation and temperatures were favourable for growth for at least 3 years following partial harvest in the studied stands (Fig. 4.4). Effects of harvest disturbances on the climate-growth relationship could be different if climatic conditions in the first few years following harvest would have been less favourable and could cause the redistribution of resources from partial harvest to become out of balance.

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CONCLUSION GÉNÉRALE

A. Principaux résultats pratiques

Le **premier chapitre** de la thèse illustre comment le simple tronquage des données dendrochronologiques peut améliorer nettement les estimations de la probabilité de mortalité. Le tronquage de séries dendrochronologiques de croissances radiales diminue l'influence des conditions environnementales – qui peuvent varier depuis la mort des arbres échantillonnés et le moment de l'échantillonnage – sur les estimations des probabilités transversales[2] de mortalité. Les estimations deviennent alors plus robustes, une qualité intéressante surtout quand on vise une paramétrisation d'un modèle de simulation forestière avec les paramètres estimés. Quoique d'autres méthodes existent pour tenir compte des influences environnementales sur les estimations de probabilités, ces méthodes utilisent de la modélisation (ex. Pedersen 1998) et introduisent ainsi davantage d'incertitude dans les estimations. L'étude sur le tronquage au chapitre un constitue une **contribution importante** à la discipline puisque cette méthode s'avère une approche simple qui permet une évaluation plus robuste de la probabilité de mortalité chez les arbres.

Le **deuxième chapitre** confirme que le système de classification des arbres développé au Québec à des fins de sélection de tiges pour la coupe de jardinage permet de bien caractériser la vigueur physiologique des arbres. Ainsi, ce chapitre apporte des **informations essentielles** pour les aménagistes de la forêt feuillue québécoise mais les résultats obtenus peuvent être adaptés à d'autres milieux forestiers. Nous avons en effet trouvé une bonne correspondance entre les différentes classes proposées par le système de classification basé sur les défaults externes des arbres et notre mesure de la vigueur des arbres basée sur les probabilités longitudinales de survie. Toutefois, le classement des arbres situés entre les deux extrêmes, c'est-à-dire les arbres vigoureux mais avec défauts et les arbres en déclin 'modeste', est plus ambigü. Évidemment, les probabilités longitudinales de survie comme mesure de vigueur ne peuvent refléter que les défauts pathologiques, c'est-à-dire, les maladies qui se traduisent en

[2] Contrairement aux estimations longitudinales de probabilité de mortalité, les estimations transversales sont ponctuelles et produisent des estimés valides à un moment donnée d'une série chronologique.

une diminution de la croissance radiale. Toutefois, dans le cas des deux classes intermédiaires, les critères de classification ne sont pas toujours de cette nature ce qui peut expliquer l'ambiguïté de la classification.

Aux **chapitres trois et quatre**, nous avons démontré que la proximité aux sentiers de débardage et le degré d'ouverture du couvert associés aux perturbations de la coupe n'ont pas d'impact négatif sur la croissance et la vigueur des arbres et ne causent pas de stress hydrique détectable chez les arbres résiduels. Par contre, les épisodes de défoliation par la livrée des forêts ont provoqué des diminutions importantes de la croissance et de la vigueur et elles ont vraisemblablement eu un rôle de facteurs prédisposants et incitants dans le déclin et la mort de l'érable à sucre suite à la coupe de jardinage. Également, les défoliations ont causé la mobilisation de réserves de carbone pour refaire le feuillage consommé par les insectes tel qu'exprimé par une diminution de $\delta^{13}C$.

Ces deux derniers chapitres constituent des **apports importants à nos connaissances** car ils ont démontré que le rôle d'un vecteur de stress ne dépend pas de sa durée, tel que stipulé par Manion (1991) mais seulement de sa sévérité. Les études de la mortalité des arbres basées sur le modèle de Manion (1991) assument généralement qu'un facteur prédisposant agit de manière diffuse et à long terme, comme la compétition ou la pollution atmosphérique (ex. Pedersen 1998, van Mantgem et al. 2003). Notre étude montre clairement que l'action peut être ponctuelle et sa sévérité ne dépend pas de la nature du vecteur mais plutôt de la capacité de l'arbre de répondre à cette action.

De manière générale, ces deux chapitres fournissent des **informations intéressantes** quant à l'impact de la coupe sur le milieu forestier. La circulation de la machinerie ne semble pas avoir causé de dommages sévères aux racines fines ou celles-ci ont pu être rapidement renouvelées grâce aux conditions climatiques favorables. Aussi, la compaction observée même 11 ans après coupe n'a pas entravé la capacité d'absorption des arbres au point de causer des diminutions de croissance. En fait, les perturbations de la coupe n'ont pas eu d'impact négatif sur l'état hydrique des arbres.

Un **aspect intéressant** de notre étude a été l'utilisation de SORTIE pour les estimations rétrospectives de la lumière. Nos résultats, l'augmentation observée de la croissance des arbres associée à l'augmentation estimée de la disponibilité de lumière, confirment la

validité de cette méthode. Notre étude contribue donc à ouvrir la voie pour des études rétrospectives de la mortalité d'arbres où la disponibilité de lumière joue un rôle dans le déclin comme, par exemple, par l'intermédiaire de la compétition.

B. Interprétation des résultats

Notre étude avait comme objectifs (1) d'investiguer des pistes d'explication pour les taux élevés de mortalité observés dans des érablières après coupe de jardinage et (2) améliorer la comptréhension des mécanismes et processus de la mortalité chez les des arbres en général. Nos résultats nous permettent de répondre aux questions de recherche énoncées dans l'introduction.

Plus spécifiquement, nos résultats indiquent qu'il est peu probable que le système de classification *présentement* en vigueur au Québec soit la source d'une mortalité élevée des arbres laissés sur pied suite à la coupe. Par contre, ce n'est pas ce système de classification qui a été utilisé dans les peuplements affectés par des taux élevés de mortalité. Étant donné qu'il a été impossible de classifier rétrospectivement les arbres récoltés lors de la coupe en 1993-94, cette question demeura inévitablement sans réponse. Toutefois, considérant l'ambiguïté de l'ancien système de classification (Meunier et al. 2002), il est concevable qu'une partie de cette mortalité découle d'une mauvaise sélection d'arbres. Ceci semble d'autant plus vraisemblable que l'ensemble de nos résultats ne donne pas d'autres indications sur les vecteurs potentiels de cette mortalité liée à la coupe. Toutefois, ladite ambigüité était également la raison pour laquelle nous n'avons pas inclus l'ancienne classification dans nos analyses.

Toutefois, même dans le cas des arbres moribonds, la classification sous-estime l'espérance de vie des arbres. Il est donc important de considérer la classification comme un outil valable pour le choix de tiges en ce qui concerne leur potentiel de résister à d'autres stress. Mais, quand le choix des arbres vise à éliminer les 'pertes potentielles' qui pourraient survenir dues à la mortalité des arbres avant la prochaine intervention (habituellement à tous les 20 à 25 ans), la classification ne peut pas donner des indications valables. Il ne serait certainement pas justifié de récolter les arbres moribonds seulement pour éviter leur perte

prématurée due à une mortalité imminente. De plus, ces arbres peuvent, malgré leur vigueur plus faible, encore jouer un rôle important en aménagement forestier. Par exemple, ces arbres pourraient servir pour plusieurs années comme arbres semenciers afin d'assurer la régénération du peuplement. Ainsi, l'enlèvement systématique d'arbres de la classe des moribonds n'est certainement pas souhaitable et devrait être évalué avec jugement par un forestier d'expérience.

Les perturbations associées à la coupe, même pour des arbres fortement perturbés, n'ont pas engendré d'impacts négatifs sur la croissance ou la vigueur des arbres, du moins sous les conditions environnementales rencontrées dans cette étude. L'absence d'une telle réponse chez les arbres et dans les sites à l'étude pourrait être reliée aux conditions météorologiques favorables qui ont prévalu dans les années suivant la coupe de jardinage de 1993-94 (Fig. 3.4). La croissance radiale d'essences feuillues peut être 2 à 3 fois plus élevée dans les années de forte précipitation par rapport aux années plutôt sèches (Hanson et al. 2001) et ces bonnes conditions de croissance pourraient se traduire par un rétablissement rapide du système racinaire et un contre-balancement des impacts négatifs de la machinerie chez les arbres affectés. Le taux de renouvellement des racines fines dans des érablières au Michigan a été estimé à 5,5 à 8 mois (Hendrick & Pregitzer 1992). Sous de bonnes conditions de croissance, le renouvellement de racines endommagées par la machinerie ou l'augmentation de la densité de racines fines en réponse à un appel d'eau plus fort par l'ouverture soudaine de la canopée pourrait être ainsi réalisé dans la première saison de croissance suivant la coupe. Selon nos données de croissance radiale, tout changement de l'approvisionnement en eau (compaction du sol, dommages au racines) ou de la demande en eau (exposition soudaine à la lumière) semble être contrebalancé dans l'année suivant la coupe : les croissances augmentent, pour les arbres ayant subi les deux perturbations, légèrement en 1994 (rétablissement des racines fines) et fortement en 1995 (meilleure croissance car plus de lumière mais maintenant sans contraintes hydriques).

Basé sur nos résultats des analyses isotopiques, nous pouvons conclure que la circulation de la machinerie n'a pas causé de contraintes hydriques à la croissance des arbres. Ainsi, les perturbations par la machinerie n'ont pas diminué la disponibilité en eau dans le sol ni l'absorption d'eau par les arbres à un niveau nuisible pour leur croissance. Quoique des

mesures de la résistance à la pénétration du sol nous indiquent la persistance de la compaction du sol même 11 ans après la coupe (Fig. 4.7), cette compaction ne semble pas avoir des impacts négatifs sur la croissance des arbres contrairement à ce qui a été observé ailleurs (Wronski 1984, Helms &Hipkin 1986, Clayton et al. 1987, Smith & Wass 1994, Souch et al. 2004, mais voir aussi Miller et al. 1996, Ares et al. 2005).

Nos résultats montrent également que l'augmentation soudaine de la lumière n'entraîne pas de 'choc d'éclaircie' comme il a été observé dans de jeunes arbres après éclaircie (ex. Staebler 1956, Harrington & Reukema 1983). Les érables dans notre étude n'ont pas manifesté de réponses retardées à l'éclaircie (Jones & Thomas 2004) mais plutôt une augmentation immédiate de la croissance radiale. Cette augmentation semble intuitivement liée à une augmentation du taux photosynthétique du feuillage d'ombre dégagé par la coupe (Jones & Thomas 2007) mais pourrait être causé également par la libération d'autres ressources édaphiques tels l'eau ou des nutriments (Aussenac 2000). Toutefois, l'interaction entre la libération des ressources édaphiques par la coupe et l'augmentation de la croissance est encore mal connue (Singer & Lorimer 1997).

L'impact positif de l'augmentation de la disponibilité de lumière sur les croissances radiales débute dans la deuxième année après la coupe et persiste pour environ quatre ans. La fermeture graduelle de la canopée (Runkle & Yetter 1987, Choi et al. 2001) semble causer un rétablissement de la compétition pour les ressources (eau, nutriments, espace) après cette période ce qui pourrait expliquer l'atténuation de l'augmentation de la croissance radiale.

La combinaison des perturbations (machinerie + lumière) n'a pas engendré de diminution de croissance ou de vigueur, ni de stress hydrique. Évidemment, un effet additif pourrait se développer seulement quand les deux perturbations exercent des impacts négatifs sur l'état hydrique des arbres. Quoique l'augmentation de la lumière ait eu tendance à causer des contraintes hydriques à la croissance (Fig. 4.3), les perturbations du sol n'ont pas entravé l'approvisionnement en eau suffisamment pour réduire le taux photosynthétique tel qu'indiqué par l'augmentation de la croissance suivant la coupe (Fig. 4.1 & Fig. 4.2).

Les défoliations par la livrée des forêts, notamment la défoliation de 1988, ont eu un impact important sur la vigueur des arbres, indiqué par la diminution sévère des probabilités de survie lors de la période de défoliation. Nos résultats concordent alors avec ceux de Gross

(1991) qui a lié des diminutions de croissance radiale et le dépérissement de la cime d'érable à sucre aux défoliations par cet insecte mais également avec Payette et al. (1996) qui ont lié le déclin massif de l'érable à sucre observé dans les années 1980 à une interaction entre les défoliations et des sécheresses.

Une première défoliation par la livrée des forêts a causé, dans les années 1970, une diminution de la vigueur de certains arbres. Ces arbres ainsi affaiblis ont été plus vulnérables à d'autres stress. Une deuxième défoliation (1986-92) a par la suite causé un déclin sévère de leur vigueur. Ces arbres ne se sont jamais remis de ce déclin et les perturbations associées à la coupe semblent avoir contribué à une accélération de leur déclin vers la mort (Fig. 3.3).

Cette dynamique de déclin concorde parfaitement avec le modèle conceptuel de déclin des arbres de Manion (1991). Pour les érables à l'étude, la défoliation de 1974-76 a joué le rôle d'un stress prédisposant qui a réduit la vigueur initiale de certains arbres et les a rendus plus vulnérables à des stress plus sévères, à des stress incitants (Fig. C1). Les perturbations de la coupe ont accéléré ce déclin en agissant comme stress contribuants.

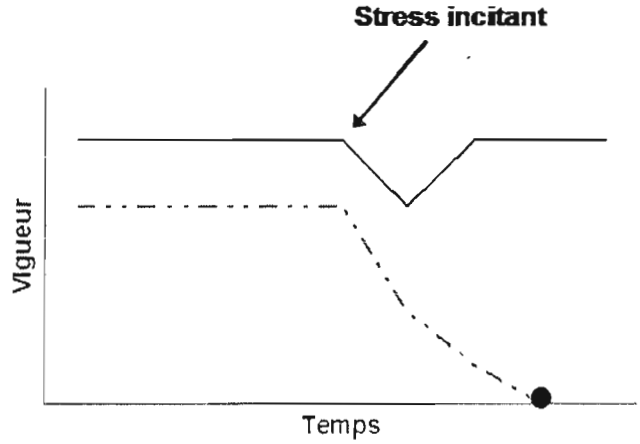

Figure C.1 Modèle conceptuel du déclin des arbres de Manion (1991). Chaque ligne représente un arbre, la différence entre les niveaux de vigueur découle de l'impact d'un stress prédisposant sur celle-ci. Le stress incitant ne cause qu'un creux temporel de la vigueur dans l'arbre en 'santé' (ligne continue) mais déclenche un déclin vers la mort (•) dans l'arbre affaibli (ligne pointillée) par le stress prédisposant. Un stress contribuant agit sur la pente du déclin vers la mort (Figure adaptée de Pedersen 1998).

Notre étude ajoute donc une composante importante aux études antérieures portant sur la mortalité des arbres : l'identification de la nature d'un stress prédisposant. Quoique Pedersen (1998) ait trouvé une dynamique de déclin similaire chez des chênes (*Quercus spp.* L.), van Mantgem et al. (2003) chez *Abies concolor* ([Gord. & Glend.] Lindl.) ainsi que Cherubini et al. (2002) chez *Pinus mugo* (Turra), dans ces cas seul les stress incitants avaient été identifiés. Ceux-ci correspondaient respectivement à des sécheresses, au passage du feu (roussissement de la cime) et aux infections fongiques de *Heterobasidion annosum* ([Fr.] Bref.). Toutefois, dans ces études, la nature des stress prédisposants n'avait pas été identifiée mais seulement assumée comme étant des perturbations diffuses, agissant à long terme, telles la pollution atmosphérique ou la compétition (Fig. I.1).

Notre étude montre qu'un seul agent de perturbation (livrée des forêts) causant des perturbations ponctuelles et distinctes (épisodes de défoliation) peut agir comme stress prédisposant mais également comme stress incitant. Ce n'est donc pas la nature du vecteur ni la durée de son effet, tel que stipulé par le modèle conceptuel de Manion (1991), qui

déterminent son rôle dans le déclin des arbres mais plutôt la réponse individuelle des arbres à une perturbation. Dans notre étude, seuls certains érables ont été affaiblis et donc prédisposés à d'autres stress par la défoliation de 1974-76, ce qui découlait probablement de leur faible capacité à se remettre de cette perturbation. La quantité de réserves de carbone pourrait y jouer un rôle causal (Parker & Houston 1971) ce qui signifie que seuls les arbres ayant amplement de réserves seraient capables de recouvrer complètement leur état de santé après la défoliation. Puisque l'épuisement des réserves de carbone diminue la capacité des arbres à se défendre contre d'autres attaques et les rend davantage vulnérables à d'autres défoliations (Dunn et al. 1987, Renaud & Mauffette 1991), la défoliation de 1974-76 a seulement agit comme stress prédisposant sur les arbres qui, pour des raisons inconnues (ex. capacité de défense des arbres, variabilité spatiale de la densité de population d'insecte), n'ont pas réussi à refaire leur réserves épuisées. Par la suite, la défoliation plus sévère de 1986-92 a fortément réduit la vigueur de tous les arbres mais seulement pour les arbres prédisposés, cette défoliation avait l'effet d'un stress incitant.

Dans notre étude, le déclin des arbres, du déclenchement par le stress prédisposant jusqu'à leur mort, a duré environ 30 ans (Fig. 3.3). L'impact négatif des défoliations sur la croissance radiale a été, en moyenne, d'une durée de 4,6 ans (Tableau 3.2). Basé sur la durée moyenne des épidémies de la livrée, estimée à deux à trois ans (Fitzgerald 1995), et sur la comparaison entre les périodes de détection de la livrée des forêts lors des recensements gouvernementaux avec la durée des diminutions de croissance radiale (Fig. 3.2, Tableau 3.2) il semble que les arbres vigoureux absorbent l'impact des défoliations assez rapidement, soit au cours de deux à quatre ans après la fin de l'épidémie.

C. Sommaire et perspectives

Quoique notre étude a mis en lumière plusieurs aspects de la mortalité des arbres, nous ne pouvons pas expliquer, basé sur nos résultats, les forts taux de mortatlité enregistrés pour l'ensemble de la province. Toutefois, il est important de mentionner ici que le rapport dévoilant les taux de mortalité n'a pas spécifié les taux par région. Il serait donc possible que

la région sous étude n'a pas été affectée par ce phénomène et, par ce fait, notre étude ne pouvait pas identifier ses causes.

Néanmoins, nous avons pu démontrer que le déclin suit le modèle conceptuel de Manion (1991) et constitue un processus progressif d'une durée de quelques décennies. Des facteurs de stress interagissaient avec les arbres en diminuant graduellement leur vigueur, certains arbres pouvant recouvrer leur vigueur initiale alors que pour d'autres, le déclin se poursuivait jusqu'à leur mort.

Les défoliations par la livrée des forêts ont eu un impact beaucoup plus sévère sur la croissance et la vigueur des arbres et ont été responsables du déclin et à la mort de certains érables. Les perturbations de la coupe n'ont eu soit aucun impact ou un impact positif sur la croissance et la vigueur des arbres. Toutefois, nous avons également démontré que l'absence d'impact de la coupe sur l'état hydrique des arbres pourrait découler des conditions climatiques favorables. Ainsi, il serait intéressant d'étudier la contribution des conditions climatiques sur les résultats obtenus. Quel impact les perturbations de la coupe auraient-elles si la coupe avait eu lieu au cours d'une année suivie d'une sécheresse estivale? Similairement, nous avons indiqué au chapitre trois que les caractéristiques des sols (i.e., sols sablonneux peu susceptibles à la compaction) dams la région d'étude pourraient expliquer l'absence d'impact de la circulation de machinerie sur les croissances radiales. Alors, est-ce que les résultats obtenus seraient différents dans des régions ayant des sols différents?

Également, pourquoi certains arbres se sont échappés de l'impact négatif des défoliations de la livrée des forêts? Pourquoi ces défoliations ont-elles déclenché le déclin seulement dans certains arbres? Est-ce que ces arbres ont été capables de se défendre activement en synthétisant des produits de défense (Barbehenn et al. 2005)? Ou est-ce que les arbres ont échappés à la défoliation par une désynchronisation entre l'ouverture des bourgeons et l'éclosion des œufs de la livrée (Tikkanen & Julkunen-Tiitto 2003)?

Ces questions devraient être abordées afin de clarifier davantage les processus de la mortalité de l'érable à sucre mais également pour mieux comprendre le déclin et la mortalité des arbres en général.

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ANNEXE 1: Analyses de corrélation et de fonction de réponse complémentaires au chapitre quatre

Tel que suggéré par le président du Jury, le Dr. Yves Bergeron, nous avons effectué une analyse complémentaire au chapitre quatre. Selon ces suggestions, la considération des conditions climatique de l'année précédente à la période de croissance pourrait avoir une influence sur la croissance des arbres. Cette suggestion est basée sur le fait que les séries de données dendrochronologiques sont souvent caractérisées par une autocorrélation (i.e., corrélation inter-annuelle). Cette autocorrélation découlerait de la mise en réserve de produits de la photosynthèse lors de la saison de croissance et de la mobilisation de ces réserves au printemps subséquent afin d'approvisonner le débourrement des bourgeons et la croissance printanière avec du carbone.

Toutefois, notre analyse initiale au chapitre quatre a été contrainte par le nombre d'années de croissance sous analyse (le nombre de mois doit être égale ou supérieur à 1,5 fois le nombre de prédicteurs, c.-à-d., le nombre de mois), alors une analyse complète couvrant les deux saisons de croissance a été impossible. Dans notre cas, le nombre de mois ne pouvait pas dépasser 13 (20 années communes de données de croissance et de climat). Alors nous avons décidé de faire les analyses de corrélation et de fonction de réponse complémentaires séparément pour l'année précédente.

Le tableeau A1 montre que les indices de croissance ajustés ("rescaled") ont été significativement corrélés avec la température en juin précédent pour le 'light & soil treatment' et avec la précipitation en juillet précédent pour le 'soil treatment' (pour ce dernier, le paramètre de la fonction de réponse a été également significatif). Ces résultats sont intuitivement logiques : la température en juin peut être limitante à la croissance au moment que les sols sont encore saturés d'eau. Ainsi, des températures en juin sont positivement corrélées avec la croissance. En juillet, après l'épuisement des réserves d'eau du sol, la précipitation devient limitante à la croissance. Ces relations sont particulièrement déterminant pour les deux traitements affichant des augmentations importantes de croissance radiale suite à la coupe (Figure 4.2).

Table A1 Complementary correlation (COR) and response function (RF) analysis of rescaled ring-width indices and climate data (see chapter 4, Figure 6) for the previous year (May to September). Bold values indicate significant ($p < 0.05$, 95% percentile range of the bootstrapped distribution) correlation coefficients or response function parameter estimates.

		Treatment							
		No		Light		Light & soil		Soil	
	Month	COR	RF	COR	RF	COR	RF	COR	RF
Temperature									
	MAY	-0.120	-0.094	-0.273	-0.230	-0.110	-0.125	-0.035	-0.055
	JUN	-0.073	-0.064	0.326	0.298	**0.421**	0.357	0.184	0.198
	JUL	-0.077	-0.050	0.005	-0.033	0.026	-0.029	-0.309	-0.244
	AUG	-0.058	-0.007	-0.090	-0.119	-0.062	-0.090	-0.218	-0.144
	SEP	-0.223	-0.153	0.147	0.103	0.013	0.013	-0.213	-0.127
Precipitation									
	MAY	0.261	0.138	-0.009	0.000	-0.051	-0.030	0.067	0.009
	JUN	0.313	0.243	0.270	0.190	0.210	0.153	0.163	0.131
	JUL	0.322	0.209	0.148	0.168	0.129	0.153	**0.468**	**0.417**
	AUG	0.185	0.174	-0.191	-0.159	-0.195	-0.169	-0.118	-0.106
	SEP	-0.034	-0.029	0.190	0.215	0.195	0.213	0.202	0.244